UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFETS DU CLIMAT ET DES RÉGIMES DE PERTURBATIONS SUR LA STRUCTURE, LA CROISSANCE ET LA RÉGÉNÉRATION FORESTIÈRE DES PEUPLEMENTS DE PEUPLIER FAUX-TREMBLE (*Populus tremuloides* Michx.), LE LONG D'UN GRADIENT EST-OUEST DANS LA FORÊT BORÉALE DU CANADA

THÈSE

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La présente thèse se compose d'une introduction générale, de trois chapitres qui décrivent la recherche qui a été menée durant ce doctorat et d'une conclusion générale. Les trois chapitres sont présentés sous forme d'articles scientifiques dont le premier est déjà publié, le second est engagé dans le processus de publication, et le troisième est en préparation pour la soumission. Mes directeurs de recherche sont des co-auteurs de différents chapitres, dont j'ai été le principal artisan que ce soit dans le choix des analyses statistiques utilisées que dans la rédaction. Chaque chapitre est une réponse à un objectif de recherche bien determiné, et comprend (*i*) une introduction qui met en contexte la question examinée, la problématique et les objectifs poursuivis; (*ii*) les matériels et méthodes utilisés; (*iii*) les résultats de la recherche et une discussion des résultats obtenus, en lien avec les mesures environnementales.

Le premier chapitre, intitulé "*Conifer recruitment in trembling aspen* (*Populus tremuloides* Michx.) *stands along an east-west gradient in the boreal mixedwoods of Canada*", a été publié en 2014 dans la revue *Forests, 5, 2905-2928*. Les coauteurs sont les co-superviseurs de cette thèse Yves Bergeron et Alain Leduc. Ces derniers sont à l'origine de la recherche, et ont collaboré à l'interprétation (discussion) des résultats, et à la révision du texte.

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Le troisième chapitre, intitulé "*Impact of climate and soil properties on aspen* (*Populus tremuloides* Michx.) *growth, along an east-west transect in Canada's forest*", a été soumis pour publication en mai 2016 dans la revue *Canadian Journal of Forest Research*. Pour ce chapitre, les autres coauteurs sont Alain Leduc, Han Y.H. Chen et Yves Bergeron.

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RÉSUMÉ

La présente recherche doctorale est une composante d'un vaste projet de recherche visant à analyser les incidences du climat et des régimes de perturbations sur la structure et la dynamique des peuplements de peuplier faux-tremble au Canada, dans un contexte des changements climatiques.

En Amérique du nord, les écosystèmes forestiers sont particulièrement sensibles aux variations du climat. Ce dernier affecte les processus écologiques et les régimes de perturbations naturelles agissant à différentes échelles temporelles et spatiales. Le réchauffement climatique projeté et l'altération du régime des précipitations qui lui est associé, sont susceptibles d'entraîner une aggravation de la sécheresse et du stress de chaleur dans les latitudes nordiques; et par conséquent, des augmentations régionales des taux de perturbations naturelles et des changements régionaux dans la croissance et la productivité des forêts. Dans les forêts du Canada, les impacts des changements climatiques en cours se font déjà sentir, à travers notamment une tendance globale à l'augmentation des précipitations dans la partie Est de la zone boréale, et des épisodes de sécheresses importantes dans la zone boréale intérieure de l'Ouest canadien. Ces changements sont prévus pour se poursuivre dans le futur, avec possiblement aussi des sécheresses dans la partie Est si l'augmentation des précipitations sera probablement plus que compensée par la demande en évaporation associée à la hausse des températures.

Dans un contexte de gestion écosystémique, qui tient compte de variations climatiques futures en région boréale, le maintien de fonctions et de l'intégrité écologique des forêts représente un défi pour les gestionnaires. Le but principal de cette recherche doctorale consiste à analyser les effets de la variabilité du climat et des régimes de perturbations (naturelles et anthropiques) sur la dynamique forestière du peuplier faux-tremble ou tremble (*Populus tremuloides* Michx.), en échantillonnant le long d'un gradient longitudinal (gradient de « précipitation »), traversant toute la forêt boréale du Canada. Cette recherche doctorale se divisait en trois objectifs spécifiques présentés en chapitres : (1) examiner l'occurrence et l'abondance de la régénération des différentes espèces de conifères (épinette blanche, épinette noire et sapin baumier) dans les peuplements dominés par le tremble, le long d'un transect Est-Ouest dans la forêt boréale mixte du Canada; (2) analyser les effets

du climat et des régimes de perturbations sur la structure et la composition des peuplements dominés par le tremble, à travers le gradient de l'étude; et (3) examiner les relations entre la croissance du tremble et les facteurs environnementaux, incluant le climat et les propriétés physiques et chimiques du sol minéral, le long du gradient de l'étude. Les peuplements de l'étude se retrouvent dans un large éventail de conditions climatiques, de régimes de perturbations et d'historique d'aménagement.

En dépit du contraste marqué dans les conditions climatiques et les régimes de feux entre l'Ouest (plus sec, avec des grands feux récurrents) et l'Est (plus humide, avec des cycles de feu relativement longs) de la forêt boréale du Canada, les principaux résultats de cette recherche montrent que : (*i*) dans le premier chapitre, la régénération conifférienne était présente dans le sous-couvert des tremblaies tout au long du gradient de l'étude, excepté dans les peuplements affectés par les activités anthropiques. Toutefois, le patron de distribution spatiale de l'abondance et l'occurrence a varié d'une espèce de conifères à l'autre; (*ii*) dans le deuxième chapitre, en classant les peuplements de l'étude parmi trois principaux types structuraux (juvénile, intermédiaire et mature) et de composition (tremblaies pures, presque pures et moins pures), le patron de distribution de types structuraux et compositionnels dans les peuplements de tremble n'était pas très différent entre les régions Est et Ouest du gradient de l'étude. Cependant, les principaux facteurs qui modèlent le patron de distribution observé dans la structure et la composition des tremblaies étaient différents entre les deux régions; (*iii*) dans le troisième chapitre, en utilisant l'indice de qualité de station comme une mesure de la croissance en hauteur du tremble en terme de productivité, il a été observé que la productivité du tremble a varié différemment d'un endroit à un autre dans la zone d'étude, dépendamment de l'interaction entre le climat régional et les conditions du sol. Toutefois, la productivité du tremble était meilleure dans les parties Est et Ouest du gradient longitudinal de la forêt boréale du Canada, tandis qu'elle a diminué dans la partie centrale du gradient de l'étude. L'augmentation du déficit en eau a été identifiée comme un facteur majeur affectant négativement la productivité du tremble dans la zone d'étude, en interaction avec la fertilité du sol (disponibilité en phosphore). Malgré les projections climatiques indiquant une augmentation de la température et des précipitations dans certaines régions boréales du Canada, les augmentations dans les précipitations prévues dans les plaines boréales (zone intérieure de l'ouest canadien) seraient insuffisantes et ne pourraient pas totalement compenser l'augmentation de l'évapotranspiration induite en raison des températures accrues qui sont prédites. Cet effet de sécheresse est prévu pour être plus important dans la partie Ouest de la forêt boréale, et plus modeste dans la partie Est de la forêt boréale du Canada. Outre le fait que le déficit en eau représente un important facteur contrôlant la productivité du tremble, l'analyse de régression multiple a révélé que les conditions de sécheresse sévère sont également un déterminant majeur dans le recrutement de la régénération coniferienne le long du gradient longitudinal dans la forêt boréale mixte. Ce résultat suggère également que la récurrence des feux sévères qui découle des conditions de

sécheresse du milieu pourrait, par conséquent, conduire à une augmentation de l'abondance relative des espèces pionnières feuillues tel que le tremble dans les couverts forestiers boréaux, au détriment de celle des espèces de fin de succession non adaptées à la perturbation du feu, sous les conditions climatiques futures. Une altération du régime naturel de feux qui résulterait en une augmentation dans la taille, la fréquence et la sévérité des feux de forêt dans le futur, pourrait conduire vers une simplification de la structure et de la composition des paysages forestiers en région boréale, en raison du redémarrage fréquent de la dynamique successionnelle. A cet égard, la capacité des écosystèmes de la forêt boréale à fournir des biens et services tels que le bois ou la biodiversité peut devenir de plus en plus variable, notamment suite à la diminution de la proportion des vieilles forêts à structure complexe. Par ailleurs, cette recherche a également montré qu'il était difficile d'interpréter les impacts de changements climatiques sur le recrutement des conifères ainsi que la structure et la composition des peuplements de tremble, sans tenir compte des effets superposés des activités anthropiques. Les résultats de ce doctorat ont des implications importantes pour les utilisateurs de la ressource, afin de mieux cibler les stratégies sylvicoles qui tiennent compte des variations locales et régionales dans les conditions environnementales en forêt boréale du Canada.

Mots-clefs : Peuplier faux-tremble, changements climatiques, régimes de perturbations, forêt boréale, régénération coniferienne, structure et composition du peuplement, productivité forestière, propriétés du sol

INTRODUCTION GÉNÉRALE

Les écosystèmes forestiers boréaux sont étroitement liés au climat, à la fois directement par les effets de la température et des précipitations, et indirectement par les effets des régimes de perturbations (Gauthier *et al.*, 2014). Les projections climatiques futures prévoient une augmentation des températures moyennes (IPCC, 2007) et de la sévérité de la sécheresse dans les régions boréales (Girardin and Mudelsee, 2008); et subséquemment, une altération du régime naturel de feux qui se traduirait en une augmentation dans la taille et la sévérité des feux de forêt (Flannigan *et al.*, 2005; de Groot *et al.*, 2009; Bergeron *et al.*, 2010; van Bellen *et al.*, 2010). Ces changements sont susceptibles d'affecter significativement le processus de régénération des espèces, la croissance et la dynamique forestière dans la région boréale (Papadopol, 2000; Frelich, 2002; Gauthier *et al.*, 2014). Les répercussions des changements climatiques sur les caractéristiques forestières peuvent varier selon la composition et les conditions du site (Messaoud and Chen, 2011). En outre, des études récentes indiquent qu'une augmentation de l'activité du feu en région boréale, résultant du réchauffement climatique, se traduirait par une expansion de forêts de feuillues et une réduction du couvert de conifères (e.g. Tang *et al.*, 2012; Kelly *et al.*, 2013) et une simplification de la structure et composition forestière dans les paysages boréaux (Boucher *et al.*, 2003; Shorohova *et al.*, 2009). Dans un tel contexte, les impacts actuels et futurs des changements climatiques représentent donc un véritable défi pour l'aménagement forestier et le maintien de l'intégrité écologique des écosystèmes forestiers boréaux. La gestion des forêts aura lieu dans les environnements décisionnels complexes, dynamiques, et incertains (Gauthier *et al.*,

2014). La mise en œuvre des stratégies sylvicoles adéquates pour l'adaptation et/ou l'atténuation des impacts de ces changements requiert une meilleure connaissance de la nature actuelle de la dynamique successionnelle des écosystèmes forestiers boréaux (Bergeron *et al.*, 2001) et l'importance relative de différents patrons spatio-temporels de la dynamique des forêts (Bergeron *et al.*, 2014). Cette recherche doctorale vise donc à mieux comprendre les relations entre les régimes de perturbations, le climat, la croissance et la dynamique du peuplier faux-tremble ou tremble au Canada. Les impacts actuels et futurs des changements climatiques se traduisent notamment par une augmentation des précipitations dans la partie Est de la zone boréale, et des sécheresses importantes dans la zone boréale intérieure de l'Ouest canadien (Hogg and Bernier, 2005; Price *et al.*, 2013; Tardif and Bergeron, 1997). Ces impacts induisent des augmentations régionales dans les taux de perturbations naturelles (feu et épidémies d'insectes) et des changements régionaux dans la croissance et la productivité des forêts (Tardif and Bergeron, 1997; Hogg *et al.*, 2008; Flannigan *et al.*, 2005; de Groot *et al.*, 2009; Bergeron *et al.*, 2010; Gauthier *et al.*, 2014). Le contraste entre les régions les plus humides et les plus sèches devrait être de plus en plus prononcé, sous les conditions climatiques futures (Girardin and Mudelsee, 2008; IPCC, 2013). Dans la présente recherche, il s'agit d'évaluer les effets de la variabilité climatique et de régimes de perturbations sur les aspects touchant à la dynamique du peuplier faux-tremble, en échantillonnant le long d'un gradient longitudinal d'un bout à l'autre de la forêt boréale mixte du Canada. Longitudinalement, le plus important changement à travers la forêt boréale d'Amérique du nord est le changement dans les précipitations et le régime de feux subséquent (Hart and Chen, 2006).

0.1 Bref aperçu de la forêt boréale mixte du Canada

Le sud de la forêt boréale canadienne est dominé par la forêt boréale mixte, qui forme une ceinture large qui s'étend sur six provinces (Québec, Ontario, Manitoba,

Saskatchewan, Alberta et Colombie-Britannique) et deux territoires (Yukon et Territoires du Nord-Ouest) (Bergeron *et al.*, 2014). Cette région est caractérisée par une mosaïque complexe de types de forêts, qui varie à la fois en structure et dans la proportion relative des espèces feuillues et de conifères. Cet écosystème très productif et diversifié est influencé par un fort gradient est-ouest dans le climat, les conditions édaphiques, et les régimes de perturbations (Bergeron *et al.*, 2014). Le climat influence considérablement les régimes de perturbations naturelles qui se produisent et interagissent à différentes échelles spatio-temporelles (Bekker and Taylor, 2001). La forêt boréale dans l'Ouest canadien est soumise à des masses d'air plus chaud et sec (Chhin *et al.*, 2008), se caractérisant par une récurrence courte des larges et sévères incendies (Johnson *et al.*, 1998); alors que la forêt boréale dans l'Est du Canada est caractérisée par un climat maritime et des incendies qui ont tendance à être moins fréquents, moins grands et de sévérité variable (Bergeron *et al.*, 2002; Bergeron and Fenton, 2012). Les différences dans la fréquence et la taille de feux influencent fortement la composition, la structure et la dynamique de la végétation forestière (Bergeron and Dansereau, 1993; McIntire *et al.*, 2005; Johnstone and Chapin, 2006a; Bouchard and Pothier, 2008; Brassard *et al.*, 2008; Johnstone *et al.*, 2010). Les régimes de perturbation sont capables de redémarrer la succession forestière (Chen and Popadiouk, 2002; Vaillancourt *et al.*, 2009). Outre le feu, les épidémies d'insectes sont parmi les principales perturbations naturelles en forêt boréale (Hunter, 1993; Chen and Popadiouk, 2002), et dépendent prioritairement de la composition forestière au niveau du peuplement et du paysage (Campbell *et al.*, 2008; Colford-Gilks *et al.*, 2012; Nixon and Roland, 2012).

0.2 Importance écologique et économique du tremble

Ce doctorat cible les peuplements de peuplier faux-tremble (*Populus tremuloides* Michx.), dans des écosystèmes qui sont largement contrôlés par des perturbations

naturelles. Le tremble est l'espèce arborescente la plus largement répandue en Amérique du Nord (Burns and Honkala, 1990); une des rares espèces à avoir une distribution transcontinentale, et cela d'une manière continue. Cette espèce montre de grandes amplitudes écologiques, en raison de sa large distribution géographique, la gamme des sites et des climats où elle est présente, ainsi que son association avec de nombreuses espèces différentes (Chen *et al.*, 2002). On le retrouve sur une large gamme de régimes d'humidité du sol, de très sec à très humide, et de régimes de nutriments, de très pauvre à très riche (Hogg *et al.*, 2005). La capacité de cette essence à dominer les premières étapes de la succession forestière et à se maintenir le long d'un gradient secondaire de celle-ci est liée à l'abondance et la dispersion à grande distance de ses graines; mais essentiellement à son mode de reproduction végétatif, par drageonnement racinaire (Cumming *et al.*, 2000). En forêt boréale mixte, les peuplements de tremble s'établissent généralement immédiatement après un événement de feu sévère, pour faire place dans la succession naturelle à des peuplements mixtes et conifériens (Oliver *et al.*, 1996; Bergeron, 2000; Gauthier *et al.*, 2000; Bergeron *et al.*, 2004; Hart et Chen, 2008). Différentes trajectoires de remplacement des espèces de la canopée sont possibles au cours du développement de peuplements, dépendamment de conditions environnementales locales tels que le climat, les régimes de perturbations et le sol (Bergeron, 2000; Chen and Popadiouk, 2002; Hart and Chen, 2006; Bergeron and Fenton, 2012; Taylor and Chen, 2011). L'origine des perturbations, leur fréquence, leur intensité et leur étendue constituent autant de facteurs qui influencent le maintien et l'abondance relative du tremble dans le paysage (Bergeron *et al.*, 2014).

Outre son importance écologique (en fournissant des services écosystémiques tels que l'habitat pour la faune), le tremble est devenu une ressource importante pour l'industrie forestière depuis les années 1980 (Peterson and Peterson, 1992). Son bois tendre est l'un des plus utilisés aujourd'hui dans l'industrie des pâtes et papiers ou encore, dans celle d'autres produits du bois (contreplaqué, allumettes, composants de

palettes,etc). Les efforts de compréhension de l'influence de conditions environnementales sur la croissance et la dynamique du tremble ont augmenté au cours des dernières décennies, d'une part en raison du potentiel de l'espèce comme une source de matière ligneuse et d'autre part du rôle croissant des feuillus dans la gestion sylvicole (Chen *et al.*, 2002; Hogg *et al.*, 2008; Gauthier *et al.*, 2010; Kelly *et al.*, 2013).

Le réchauffement climatique pose un risque d'augmentation des conditions de sécheresse au cours des prochaines décennies, et qui pourrait conduire à des impacts négatifs à grande échelle sur les forêts soit directement (Barber *et al.* 2000, Hogg *et al.* 2005, 2013) ou en combinaison avec les régimes de perturbations naturelles découlant du climat régional (Flanningan *et al.* 1998). Il est montré, par exemple, qu'une baisse importante de productivité du tremble dans la zone intérieure de l'Ouest canadien serait associée à la sécheresse sévère survenue dans cette région entre 2001 à 2003 (Hogg *et al.* 2005, Hogg *et al.* 2013). Des signes de dégradation accélérée des forêts de tremble ont été également observés un peu partout en Amérique du Nord, et qui seraient attribués à l'occurrence de perturbations telles que la défoliation par la livrée de forêts (*Malacosoma disstria* Hbn.), et les événements climatiques extrêmes comme les épisodes de sécheresse et de gel-dégel (Candau *et al.* 2002, Hogg *et al.* 2002, Frey *et al.* 2004, Hogg *et al.* 2005, Hogg *et al.* 2008, Worrall *et al.* 2013).

0.3 Échelle de l'étude

Dans l'optique d'une meilleure compréhension de la réponse des forêts de tremble aux changements globaux sur le long-terme, les modèles ont besoin de refléter une large gamme de conditions environnementales qui sont pertinentes pour la croissance et la dynamique de l'espèce forestière de l'étude. C'est ainsi que la zone de notre étude s'étend sur l'ensemble de la forêt boréale mixte du Canada, en y incluant

également quelques sites de la zone des forêts parc de l'ouest Canadien dans le chapitre sur l'analyse de la croissance du tremble. Dans ce contexte de changement climatique, et leurs conséquences sur les régimes de perturbations naturelles, la forêt boréale mixte du Canada représente un système naturel idéal pour explorer les effets de la variabilité climatique et de régimes de perturbations sur la végétation. En effet, il existe de grandes variations régionales dans les facteurs climatiques, édaphiques, topographiques et dans le risque d'incendie entre les provinces du Canada et au sein d'une même province (Environment Canada, 2013). En échantillonnant les peuplements dominés par le tremble le long du transect est-ouest pan-Canadien, une aire de répartition géographique très vaste, cela a permis de couvrir une large gamme de conditions environnementales. Les résultats de l'étude donnent un aperçu sur la façon dont les caractéristiques forestières seraient affectées dans une région donnée, si les conditions climatiques venaient à varier dans les amplitudes de celles déjà observées dans une autre région.

0.4 Objectifs et structure de la thèse

L'objectif principal de cette thèse consiste donc à analyser les effets de la variabilité du climat et des régimes de perturbations (naturelles et anthropiques) sur la dynamique forestière du peuplier faux-tremble, en échantillonnant le long d'un gradient longitudinal, dans la forêt boréale du Canada. L'échelle continentale de cette recherche doctorat représente une situation unique en Amérique du nord. Les précédentes études sur la croissance et la dynamique naturelle des peuplements de cette espèce-clé de la forêt boréale ont souvent porté sur des étendues moins vastes, comme un territoire (e.g. Chen *et al.*, 1998a; Paré *et al.*, 2001; Kabzems and Garcia, 2004; Pinno *et al.*, 2009) ou une province – ensemble des provinces (e.g. Hogg *et al.*, 2005; Huang *et al.*, 2010; Chen *et al.*, 2002; Lapointe-Garant *et al.* 2010), et souvent en suivant un gradient "nord-sud", qui est le principal gradient de température. Par

contre, sur le gradient longitudinal à l'étude, la variable climatique majeure qui varie est la précipitation. En plus de mieux observer les effets de la variabilité du climat et des perturbations naturelles sur la dynamique des peuplements de tremble, l'étude permet également de distinguer les effets locaux (peuplement) des effets régionaux (paysage). La thèse est organisée en trois chapitres, de manière suivante :

1. Analyse de la régénération conifèrienne se trouvant dans le sous-couvert des peuplements dominés par le tremble, répartis le long du transect est-ouest dans la forêt boréale mixte du Canada, en lien avec le climat et les régimes de perturbations.

2. Caractérisation de la structure et de la composition des peuplements dominés par le tremble, répartis le long du transect est-ouest dans la forêt boréale mixte du Canada, en lien avec le climat et les régimes de perturbations.

3. Analyse de l'impact du climat et des propriétés du sol sur la croissance du tremble, le long du transect est-ouest dans la forêt boréale du Canada.

Les premier et deuxième chapitres concernent exclusivement la forêt boréale mixte du Canada, en utilisant les bases de données d'inventaires forestiers disponibles dans les provinces canadiennes de l'étude. Les résultats ont été interprétés en fonction des conditions environnementales, incluant le climat, le régime naturel de feu, et les impacts anthropiques. Tandis que les données du chapitre 3 ont été recueillies sur le terrain, en échantillonnant essentiellement dans la forêt boréale continue. Toutefois, afin d'étendre le gradient climatique, nous avons également échantillonné quelques sites dans la zone des forêts parc le long de la limite septentrionale des prairies canadiennes, pour analyser la croissance du tremble. L'interprétation des résultats

était basée sur les variables climatiques et les propriétés physiques et chimiques du sol minéral.

Dans le premier chapitre, intitulé "*Conifer recruitment in trembling aspen* (*Populus tremuloides* Michx.) *stands along an east-west gradient in the boreal mixedwoods of Canada*", il s'agit d'examiner l'occurrence et l'abondance de la régénération des trois principales espèces de fin de succession (épinette blanche, épinette noire et sapin baumier) les plus communément associées avec le tremble dans les peuplements de la forêt boréale mixte. En fonction de la variabilité de régimes de perturbations, résultant de celle du climat, à travers le gradient longitudinal en forêt boréale mixte du Canada, nous avons émis les hypothèses que (*i*) la régénération coniferienne (surtout du sapin mais aussi des épinettes blanche et noire) serait plus abondante dans les tremblaies situées dans la forêt boréale de l'Est en raison de précipitations plus abondantes et, par extension, les cycles de feu plus longs qui dominent dans cette partie du gradient. La tendance de la dominance résineuse en sapin baumier peut être expliquée par les conditions climatiques plus humides et le fait que cette espèce est plus tolérante à l'ombre par rapport à l'épinette noire et à l'épinette blanche (Bergeron et Dubuc 1988; Bergeron, 2000); (*ii*) Inversement, les tremblaies situées dans la partie Ouest devraient présenter une régénération coniferienne plus éparse des trois principales espèces de fin de succession de l'étude, compte tenu des précipitations plus faibles et des feux larges et plus fréquents qui caractérisent cette partie. En effet, les conditions plus sèches ainsi que des grands feux fréquents limiteraient l'envahissement des zones brûlées par les espèces de fin de succession (Bergeron et Dubuc 1988; Johnstone and Chapin, 2006a; Martin-DeMoor *et al.*, 2010). La récurrence de larges feux sévères peut régulièrement redémarrer la succession forestière, en favorisant l'établissement des espèces intolérantes à l'ombre, limitant ainsi l'établissement et le développement des espèces intolérantes à l'ombre. Ces dernières espèces nécessitent la présence des semenciers résiduels dans les zones non touchées par le feu afin de réenvahir les sites brûlés (Bergeron, 2000; Cumming

et al. 2000; Bergeron *et al.* 2004). Ces espèces nécessitent également du temps pour recoloniser un site après le feu (Galipeau *et al.* 1997). Par contre, la proportion des tremblaies n'ayant pas de la régénération résineuse serait plus élevée dans la partie ouest comparativement à la partie Est de la forêt boréale du Canada.

Le deuxième chapitre, intitulé "*Climate and disturbance regime effects on aspen* (*Populus tremuloides* Michx.) *stand structure and composition along an east-west transect in Canada's boreal forest*", a pour objectif d'analyser le patron de distribution de types structuraux et de la dominance du tremble dans les peuplements dominés par cette espèce, le long du gradient de l'étude. Une grande variation régionale dans les facteurs climatiques et, par extension dans la fréquence de feu, existe parmi et au sein des provinces Canadiennes (Bergeron *et al.*, 2004; Boulanger *et al.*, 2012; Stocks *et al.*, 2002). Dans la forêt boréale de l'est où les cycles de feu sont généralement plus longs que dans celle de l'ouest, une grande partie de la matrice forestière avait été historiquement plus vieille que l'âge de la maturité des arbres (Kneeshaw and Gauthier, 2003). En revanche, les cycles de feu plus courts dans l'ouest de la forêt boréale résulte dans une matrice forestière dominée par des peuplements juvéniles issus généralement du feu, avec des parcelles de vieilles forêts disséminées à travers le paysage (Johnson, 1996). Basé sur les différences régionales ci-dessus, nous attendons à ce que (*i*) la partie ouest de la forêt boréale serait dominée par les tremblaies juvéniles et ayant une distribution équienne, alors que la partie est de la forêt boréale serait dominée par les tremblaies matures et ayant une distribution inéquienne en raison principalement de la présence des résineux; (*ii*) les tremblaies pures seraient plus abondantes dans la partie ouest de la forêt boréale en raison des cycles de feu plus courts, qui limiteraient les changements dans la composition de la canopée. En revanche, les cycles de feu plus longs dans l'est de la forêt boréale favoriseraient la prédominance de tremblaies ayant un sous-étage des espèces tolérantes à l'ombre dans la canopée supérieure.

Le troisième chapitre s'intitule "*Impact of climate and soil properties on aspen (Populus tremuloides* Michx.) *height growth along an east-west transect in Canada's forest*". Il vise à examiner les relations entre la croissance du tremble et les facteurs environnementaux, incluant le climat et les propriétés physiques et chimiques du sol minéral, le long du gradient de l'étude. Les écosystèmes boréaux étant très sensibles aux variations climatiques. Il existe un fort gradient de précipitations à travers le gradient de l'étude, avec des conditions plus sèches dans l'ouest et plus humides dans l'est (Environnement Canada, 2013). La partie Est du Canada se caractérise par un climat maritime (Bergeron and Flannigan, 1995), alors que la partie intérieure de l'Ouest est soumise à des masses d'air plus sec (Chhin *et al.*, 2008). Le stress hydrique (déficit en eau) a été souligné comme étant un facteur majeur contraignant la croissance et la viabilité du tremble dans la zone intérieure de l'ouest canadien (Hogg *et al.*, 2008, 2013; Worrall *et al.*, 2013). De ce qui précède, nous avons donc émis l'hypothèse que la productivité du tremble serait plus élevée dans la partie Est comparativement à celle du centre et de l'ouest du Canada. En outre, le tremble est trouvé sur une large gamme de sites ayant des attributs nutritionnels variant géographiquement (Paré *et al.*, 2001; Chen *et al.* 2002). Il est également émis l'hypothèse que la croissance en hauteur du tremble varierait parmi et au sein des régions le long du gradient longitudinal de la forêt boréale du Canada, en fonction de l'état nutritionnel du sol.

CHAPITRE I

CONIFER RECRUITMENT IN TREMBLING ASPEN (*Populus tremuloides* Michx.) STANDS ALONG AN EAST-WEST GRADIENT IN THE BOREAL MIXEDWOODS OF CANADA

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1.1 Abstract

Ongoing climate change is likely to result in shifts in successional dynamics in boreal mixedwood stands. Using data from provincial forest inventory databases, we examined the occurrence and abundance of the regeneration of various coniferous species (white spruce, black spruce and balsam fir) along an east-west Canadian gradient in aspen-dominated stands. The interpretation of the results was based on environmental conditions, including climate, natural fire regime and human impacts. We found that conifer regeneration was present in aspen stands along the entire gradient, despite differences in climatic conditions and fire regimes between the west (warmer and drier, with large recurrent fires) and east (more humid with relatively long fire cycles). However, abundance and distribution varied from one conifer species to the next. The abundance of white spruce decreased towards the eastern end of the longitudinal gradient, while balsam fir and black spruce abundance decreased towards the west. Although abundance decreased, balsam fir and black spruce regeneration was still present in western Canada. This study shows that it is difficult to interpret the effects of climate change on conifer recruitment without accounting for the superimposed effects of human activities.

Key words: trembling aspen; boreal mixedwood; coniferous regeneration; abundance; occurrence.

Résumé

Les changements climatiques en cours sont susceptibles d'entraîner des changements dans la dynamique de succession dans les peuplements de la forêt boréale mixte. A l'aide des bases de données d'inventaires forestiers des provinces du Canada, nous avons examiné l'occurrence et l'abondance de la régénération des différentes espèces de conifères (épinette blanche, épinette noire et sapin baumier) dans les peuplements

dominés par le tremble, le long d'un gradient Est-Ouest Canadien. L'interprétation des résultats était basée sur les conditions environnementales, incluant le climat, le régime naturel de feu et les impacts anthropiques. Nous avons trouvé que la régénération conifèrienne était présente dans les peuplements de tremble tout au long du gradient de l'étude, malgré les différences dans les conditions climatiques et régimes de feu entre l'Ouest (plus chaud et séc, avec des grands feux récurrents) et l'Est (plus humide, avec des cycles de feu relativement longs). Toutefois, l'abondance et la distribution ont varié d'une espèce de conifères à l'autre. L'abondance de l'épinette blanche a diminué vers l'extrémité Est du gradient longitudinal, tandis que les abondances du sapin baumier et de l'épinette noire ont diminuées vers l'Ouest. Bien que l'abondance a diminué, la régénération du sapin baumier et de l'épinette noire était encore présente dans l'Ouest Canadian. Cette étude a montré qu'il était difficile d'interpréter les effets de changements climatiques sur le recrutement des conifères, sans tenir compte des effets superposés des activités anthropiques.

Mots-clefs : peuplier faux-tremble, forêt boréale mixte, régénération conifèrienne, abondance, occurrence.

1.2 Introduction

Trembling aspen (*Populus tremuloides* Michx.) is one of the few North American tree species that has a transcontinental distribution and is found over a wide range of site conditions (Qian *et al.*, 2003). In boreal mixedwood stands, aspen usually establishes immediately after a severe fire event. Over time, successional changes shift stand composition from aspen dominated to mixed species and, finally, to stands dominated by conifers (Bergeron, 2000; Bergeron *et al.*, 2004; Gauthier *et al.*, 2000; Hart et Chen, 2008; Oliver et Larson, 1996; Qian *et al.*, 2003). Different trajectories of canopy species replacement are possible during stand development (Chen et Popadiouk 2002; Bergeron et Fenton 2012), depending on the on-site climatic and edaphic conditions, the disturbance regime, regeneration potential, biotic interactions and the life histories of the species that are present (Bergeron, 2000; Peters *et al.*, 2006).

Boreal forest ecosystems are largely controlled by natural disturbance events, especially fire (Stocks *et al.*, 2002). The fire regime, which is influenced by regional climate (Bergeron *et al.*, 1998), can significantly affect the processes of species regeneration (Hart et Chen, 2008) and the long-term development of forest stands (Taylor et Chen, 2011). Forest regeneration that is present in the understory can indicate the potential successional pathway that forest stand composition could take during its evolution (Nilsson *et al.*, 2005). In the case of aspen, its composition could be maintained as pure- and hardwood-dominated stands or a transition may occur that leads to conifer-dominated stands, depending on the local environmental conditions (climate, disturbance regime and soil). Studies indicate that large and severe fires play an important role in creating stands, with little regeneration attributable to late-successional species (Bergeron et Dubuc, 1988; Johnstone et Chapin, 2006a). Indeed, the recurrence of large and severe fires can regularly restart forest succession, favoring the establishment of shade-intolerant species, thereby limiting the

establishment and development of late-successional species. These latter species require the presence of residual seed trees preserved in unburnt areas in order to successfully reinvade a burn site (Bergeron et Dubuc, 1988; Bergeron, 2000; Cumming *et al.*, 2000; Caners et Kenkel, 2003; Bergeron *et al.*, 2004; Johnstone *et al.*, 2004); they also generally take longer to recolonize a site following fire (Galipeau *et al.*, 1997).

In the boreal forest, the nature and distribution of tree regeneration that is present at a given location is the result of climatic and physiographic conditions (Robitaille *et al.*, 1998) and the fire regime associated with this region (Flannigan *et al.*, 1998). Ongoing climate change is expected to lead to changes in the frequency and severity of fires (Bergeron *et al.*, 2010; Wotton *et al.*, 2010; Girardin *et al.*, 2013a), both at local and regional scales. This could change the current nature of the successional dynamics of boreal forest ecosystems (Bergeron *et al.*, 2001) and the relative importance of different temporal patterns across regions (Bergeron *et al.*, 2014). Knowledge of the regeneration dynamics of species along a wide gradient of environmental conditions would be essential for a better understanding of vegetation response in a constantly changing environment. Furthermore, an analysis of the distribution of vegetation that is dominated by the same canopy species at different locations across a wide and continuous forest ecosystem could help resolve the potential contrasts in the understory composition between regions, by identifying the different factors that control the variation that is observed within a region (Reyes *et al.*, 2013).

This study analyses the abundance and occurrence of recruitment of three shade-tolerant conifer species in aspen-dominated stands that are distributed along a broad gradient of climate and fire regimes across Canada. The pan-Canadian scale of this study represents a unique situation in North America. Various studies on the analysis of forest regeneration in the boreal forest are generally restricted to local or regional

scales (e.g., Lieffers *et al.*, 1996; Greene *et al.*, 1999; MacIsaac *et al.*, 2006; Lieffers *et al.*, 2008; Arbour et Bergeron, 2011).

The abundance and occurrence of coniferous regeneration should reflect the influence of environmental factors on the distribution of coniferous regeneration within aspen stands. Three conifer species are examined: white spruce or Ws (*Picea glauca* (Moench) Voss); black spruce or Bs (*Picea mariana* (Mill.) BSP); and balsam fir or Bf (*Abies balsamea* (L.) Mill.). These late-successional species are commonly found in association with aspen in boreal mixedwood stands (Bergeron et Dubuc, 1988; Robitaille *et al.*, 1998; Hart et Chen, 2006; Hart et Chen, 2008). We only target aspen stands along the study gradient, thus controlling for the effect of forest cover. This approach allows us to observe how variability in environmental conditions affected the recruitment of shade-tolerant conifers in this stand type.

Longitudinally from east to west, the precipitation regime exhibits the most prominent change across the North American boreal forest, subsequently affecting fire regime (Hart et Chen, 2006). Large regional variation in climatic factors and the risk of fire exist among and within the Canadian provinces (Stocks *et al.*, 2002; Boulanger *et al.*, 2012). The contrast in precipitation and temperature and their effects on the fire regime within eastern and western Canada are likely to have an effect on the dynamics of conifer regeneration between these two regions.

Depending upon these regional differences, we hypothesize that coniferous regeneration will be more abundant in aspen stands located in the eastern boreal forest due to higher precipitation and, by extension, the longer fire cycle that dominates this part of the transect; conversely, aspen stands in the west, which experience lower precipitation and more frequent and large fires, should exhibit lower coniferous regeneration (McIntire *et al.*, 2005; Martin-DeMoor *et al.*, 2010).

1.3 Material and Methods

1.3.1 Study area and Sample plot data

We limited stand selection to only those that were dominated by aspen and located in the boreal mixedwood ecological region of Canada (Figure 1.1). This ecosystem is influenced by a strong east-west gradient in climate, soil conditions and disturbance regimes (Bergeron *et al.*, 2014). Generally, fire frequency in the Canadian boreal forest increases from east to west (Hart et Chen, 2006), with variations in fire size, frequency and intensity across the country. The eastern part of Canada is characterized by a humid climate and by less frequent, smaller fires of variable severity (Payette, 1992; Bergeron *et al.*, 1995; Bergeron *et al.*, 2002). In contrast, the western part is subject to warmer and drier air masses (Chhin *et al.*, 2008) and is characterized by relatively large, more frequent and severe fires (Johnson *et al.*, 1998). Hart and Chen (2006) argued that there is an increase in precipitation, from about 300 to 500 mm per year in the western boreal forest to about 800–1000 mm in the eastern boreal forest, resulting in an increase in the average fire return interval from 75 years in the former to 150 years or more in the latter.

Because the delineation of the boreal mixedwood forest varies according to the authors, we extend its area by including an external buffer of 100 km on each side of the boundary (represented by the dark grey area in Figure 1.1). Thus, aspen stands that were located within the buffers were also included in the analysis.

The study was performed using decennial forest inventory databases available in the different provinces of Canada. Data selection was carried out in several steps: (1) we selected forest stands from provincial forest inventory datasets that were dominated by aspen, i.e., at least 75 % of the basal area (m^2/ha) of live and merchantable trees (dbh $\geq$ 9 cm) located in all permanent sample plots (PSPs) and temporary sample plots (TSPs) were aspen; in the case of PSPs, one set of decadal inventory measures

(the more recent one available) was retained in the selection of forest stands; (2) selected stands had to have a density equivalent to at least 400 merchantable stems per hectare, for all species combined, so as to exclude stands that would be potentially too young; (3) of the preselected stands, we retained only those that were located within the study area using ArcGIS 9. A total of 2636 stands dominated by aspen were selected for analysis (Table 1.1).

1.3.2 Estimating Abundance and Occurrence of Regeneration

Analysis of coniferous regeneration refers exclusively to sapling recruitment data (i.e., 9 cm $\geq$ dbh $\geq$ 1 cm) of the three conifer species examined (Ws, Bs and Bf). Furthermore, the abundance of coniferous regeneration within a given stand is calculated as the total number of saplings of each conifer species present in the stand. As the surveyed areas included in the study differ in size among the Canadian provinces, estimates of abundance are standardized across the gradient and expressed as the number of saplings per hectare. For a given aspen stand, the abundance of coniferous regeneration was first calculated by species (Bs, Ws and Bf) and then for all three species combined (coniferous regeneration (Conif)).

Conifer occurrence was determined by the presence/absence of the three species. To circumvent bias arising from variability encountered among provinces in terms of their surveyed areas, a detection threshold for the "presence" of a coniferous species (Ws, Bs and Bf) in a stand was set at 250 individuals (saplings) per hectare. This corresponds to a minimum threshold of detectability of one sapling in 40 m^2, which is the size of the smallest sampling area of saplings that was common to all provinces of the transect (i.e., one sapling in 40 m^2 equals 250 saplings in 1 hectare).

1.3.3 Predictive Variables

Thirteen potential predictor variables (k = 13) were selected a priori to model the distribution of the abundance and occurrence of coniferous regeneration in aspen stands distributed across the pan-Canadian study area. Predictors were considered because of their known or suspected effects on the recruitment dynamics of coniferous species in the boreal forest; these are summarized in Table 1.2. The aridity or drought index (DI) and degree-days above 5 °C (DD) were used to characterize the climatic conditions of selected sites. For each climatic variable, a 30-year average was generated in BioSIM 9 (Régnière and St-Amant, 2008) using Environment Canada data from 1981 to 2010 (Environment Canada, 2013). While DD takes into account temperature (Villeneuve, 1980), DI is a weather index that incorporates precipitation, temperature, period of sun and soil conditions, which expresses the intensity of drought (Kaennel et Schweingruber, 1995). Fire cycle (FC) data was considered in the modelling exercise as a natural disturbance event characterizing the fire regime. FC data was extracted from a map that defines areas with a homogeneous fire regime (Boulanger *et al.* 2012). We did not consider insect outbreaks as potential explanatory variables, as the work of compiling and harmonizing insect outbreak data on a pan-Canadian scale was still ongoing at the time of our study.

Like stand-replacing fires, human activities naturally promote the establishment of shade-intolerant deciduous stands (Laquerre *et al.*, 2009). Distance to the nearest main road (DistRoad) and agricultural area (DistAgri), as well as total road length per square kilometer within a radius of 15 and 25 km around the stand (DensRoad15Km and DensRoad25Km) was estimated and considered as proxies to control for the human effect on the natural environment. Anthropogenic disturbances change the landscape dynamics, acting at different scales of natural disturbances (Laquerre et al., 2009) particularly through fire occurrence (increased ignition sources). We know that changes in fire regimes as an interaction with forest harvesting have a direct impact on the composition and structure of forests (Bergeron *et al.*, 2001; Bergeron *et al.*, 2004). Distance to the nearest major river, lake or bay (DistWater) and the percentage

of hydrography (PctHydro) within a radius of 15 km, as well as physiographic regions of Canada (RegiPhysio) were added as variables describing the physical environment of the stands. Abundant hydrography can affect local climatic conditions of surrounding areas, while a major river can act as a natural barrier against forest fires (fire break). Climatic factors change with increasing latitude and longitude in the boreal forests of North America (Hart et Chen, 2006); therefore, spatial variables, such as longitude (Long), latitude (Lat) and elevation (Elev), were included in the analysis as indirect factors that should be expressed by measured climatic variables. Data on anthropogenic variables and those describing the physical environment were mainly sourced from the GeoBase of Natural Resources Canada (http://www.geogratis.ca/goegratis/DownloadDirectory?lang=fr).

1.3.4 Data analysis and Model Selection

A descriptive analysis of the abundance and frequency of occurrence for each coniferous species was carried out to illustrate their relative distribution along the longitudinal gradient. Plots were grouped by longitude in order to determine the average abundance for each longitude, while the frequencies of occurrence were estimated across a province. We then applied a linear regression (linear trend-line) on abundance data to observe trends in the distribution of coniferous species across the gradient. A similar descriptive analysis was performed on the continuous predictive variables to illustrate the variability of their distribution along the longitudinal gradient.

Multiple regression models were developed to predict the abundance of conifer regeneration using R freeware (R-Development-Core-Team, 2013). In the case of occurrence, the model was calibrated using binary logistic regression. Model selection was conducted stepwise: we began by first verifying which variable was most significantly ($p < 0.05$) related to the response variable using univariate

regression models. From the most significant variable identified, we added other variables one by one to test if, combined or not, the constructed models can explain the conifer recruitments across Canada. To avoid model over-fitting, a covariate was only retained in the model if it was significant ($p < 0.05$) in the model; and additionally contributed significantly in improving the model, with an approach based on Akaike's information criterion (AIC). The least probable assumptions (i.e., models that had at least one non-significant variable of interest at $p < 0.05$) were abandoned. The AIC has been used as a measure of the strength of evidence for each considered model in the analysis (Mazerolle, 2006). This procedure allowed preselecting a list of candidate models. Thereafter, we did a multimodel inference to compare candidate models and identify the "best" model that would best approximate reality given our dataset, calculating the delta AIC (ΔAIC) and Akaike weights (W_i), two measures that are associated with AIC (Mazerolle, 2006).

The proportion of total variance that was explained by each predictor in the best predictive model was extracted, taking into account the effect of other variables. This part expresses the proportion of variability that is provided by the variable of interest in the model; determined from the calculation of log-likelihoods (Burnham and Anderson, 2002), as in Equations (1.1) and (1.2):

$$Variance\ of\ a\ variable = 1 - R^2 \quad (1.1)$$

Or

$$R^2 = \frac{logLik3 - logLik1}{logLik2 - logLik1} \quad (1.2)$$

where, R^2 is the (pseudo) coefficient of determination; logLik1 is the log-likelihood of the null model; logLik2 is the log-likelihood of the best model; and logLik3 is the log-likelihood of the best model, from which we removed the variable of interest.

1.4 Results

1.4.1 Abundance and Occurrence of Conifer Recruitment

We observed variation in species abundance along the longitudinal gradient (Figure 1.2). There was no significant east-west gradient when considering the overall abundance of coniferous regeneration (all three species combined: Conif) in the aspen forests of Quebec and Ontario (QC and ON) compared to Alberta and British Columbia (AB and BC) (Figure 1.2a, $R^2 = 0.1$). By considering the species separately, linear regression indicates that Bf regeneration was more abundant in aspen forests that were located in eastern Canada and decreased towards the west (Figure 1.2b, $R^2 = 0.5$). The same trend was observed for Bs regeneration (Figure 1.2c, $R^2 = 0.3$), although in lower proportions relative to Bf regeneration. In contrast, the abundance of Ws regeneration was significantly higher in the western aspen forests (Figure 1.2d, $R^2 = 0.4$) and decreased towards eastern aspen forests.

The density of Bf recruitment was highest in aspen forests of QC and ON, whereas Ws was significantly higher in BC and AB. Indeed, Ws dominated the coniferous regeneration that was observed in western aspen forests. Total coniferous regeneration (Conif) was lower in the central portion of the gradient, between longitudes 95° W and 110° W, which corresponds to the range of Manitoba (MB) and Saskatchewan (SK), compared to the other provinces.

With respect to overall occurrence (Conif), coniferous regeneration was present in aspen forests along the study gradient (Figure 1.3). The relative frequencies of occurrence did not vary significantly between aspen forests in the east (QC, 32%; ON, 19%) and those in the west (BC, 33%; AB, 21%). Like the overall density, the central part of the longitudinal gradient recorded the lowest occurrence of overall coniferous regeneration (MB, 4%; SK, 5%).

In terms of species (Figure 1.3), Ws and Bs regeneration were present everywhere along the east-west gradient, while Bf regeneration was only observed in aspen forests that were located from SK eastwards. There was no Bf regeneration in aspen forests that we examined in AB and BC. However, forest inventory data from BC showed the presence of subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) regeneration in the understory of aspen forests. In addition, the frequency of Ws occurrence decreased moving towards eastern aspen forests, while that of Bs and Bf exhibited a decreasing trend towards western aspen forests. Thus, there is consistency in the patterns between density distribution (Figure 1.2) and the relative frequency of occurrence (Figure 1.3) of the examined coniferous regeneration.

1.4.2 Variability in Environmental Conditions along the Study Gradient

Analysis of climatic data shows that total annual precipitation significantly increased towards the east (Appendix A.1 - Figure A.1a, $R^2 = 0.84$), in contrast to the drought index or aridity (Appendix A.1 - Figure A.1b, $R^2 = 0.65$), which increases in the westward direction. We also observed that fire cycle (Appendix A.1 - Figure A.1c, $R^2 = 0.39$) was generally longer in the east and shorter in the west. Aspen stands in the study area were randomly located relative to the pattern of annual average temperature across the longitudinal gradient (Appendix A.1 - Figure A.1d, $R^2 = 0.13$). The stands also were randomly distributed relative to the density of roads around the aspen stands and with the distance to agricultural areas.

However, western aspen forests were located further north in the boreal forest compared to eastern aspen forests (Figure 1.1). We observed a trend where, with an increase in latitude, the distance to agricultural areas also increased, whereas road density decreased.

1.4.3 Selection of Predictive Models and Individual Effect of Variables

From the list of models that were tested (Table 1.3), Model 1 combined climate (DI), human disturbance (DensRoad25Km), and latitudinal gradient (Lat) and was the most significant for describing the distribution of the overall abundance of coniferous regeneration (Conif). Model 2, in comparison, had only climate (DI and DD) and human disturbance (DensRoad25Km). Model 1 represents about a 61% (W_i: 0.61) chance of being the best model, with 29% for Model 2 (W_i: 0.29). Other models had $\Delta AIC > 2$, indicating that they are unlikely the best fit for the data. The multiple regression procedure displayed the effect of each variable that was included in the best model (Table 1.4). Overall, abundance increases with latitude and decreased with an increase in the drought index and human impact (road density). The t-test statistics and associated p-values indicated that each retained predictor variable significantly improved the model (all $p < 0.05$).

When coniferous species were separately considered, these same variables (climate, anthropogenic and latitudinal effect) explained the abundance of white spruce (Model 1, Ws) and black spruce regeneration (Model 1, Bs). In contrast, the spatial pattern in the abundance of balsam fir regeneration was mainly explained by climate (DI) (Model 1, Bf). The model that included only the drought index had an almost 100% (W_i: 0.99) probability of being the best explanatory model for Bf, with a ΔAIC of zero.

DI had a significant negative effect on the abundance of Bs and Bf regenerations. The abundance of regeneration for both coniferous species decreased with an increase in the degree of site drought. In the case of Bs, DI was not the only major explanatory factor. Road density (DensRoad25Km) had a significant negative effect on the abundance of Bs regeneration and also a positive co-variation in abundance with latitude. The abundance of Ws regeneration significantly co-varied with latitude (Lat), but there was also a significant negative effect of annual degree-day sums (DD) and road density (DensRoad25Km).

The best predictive models that were based on occurrence (Appendix A.2 - Table A.1) were less parsimonious than those of abundance (Table 1.3). This difference resulted from the model selection approach that was used for each ecological measurement, i.e., multiple linear regression for abundance (a continuous quantitative variable) and logistic regression for occurrence (a binary variable). However, it appears that all variables in the best predictive models of abundance (Table 1.3) are included in those of occurrence (Appendix A.2 - Table A.1) for each coniferous species. Particularly, with the best predictive model, which considered all three species (Conif), the road density (DensRoad25Km) in the abundance model was replaced by the distance to agricultural area (DistAgri) in the occurrence model. For predictive variables that had been selected a priori (in Table 1.2) and that do not appear in the selected models (Table 1.3 and Appendix A.2 - Table A.1), they either did not have a significant effect on the response variable or their effect is masked (i.e., already explained) by the variables that were already in the model. This is the case of the "fire" variable (FC), which was not selected in any of the predictive models, while its impact on the occurrence and abundance of coniferous regeneration is quite obvious.

1.4.4 Variance Explained by Each Predictor Variable in the Best Model

In Table 1.5, the overall abundance model (Conif) indicates that DI explains almost 46% of the variability in the spatial pattern of the abundance distribution of coniferous regeneration. Road density (DensRoad25Km) contributes 11 % of the total explained variance, while latitude (Lat) contributes 4 %. Our results, therefore, suggest that the effect of climate is far more important than anthropogenic disturbance effects and spatial effects.

By species, the abundance of Bf regeneration was mostly explained by climate (DI), the single variable that was included in the best model. In contrast, Bs regeneration

abundance was explained by climate (DI, 40 %) and anthropogenic disturbance effects (DensRoad25Km, 29 %), together with spatial effects (Lat, 3 %). In the Ws model, anthropogenic disturbance (DensRoad25Km, 29 %) explained almost as much of the total variance as did climate (DD, 27 %) and spatial effects (Lat, 20 %). There is a consistency between the abundance and occurrence.

1.5 Discussion

Overall, there were no significant differences in the abundance of conifer recruitment (Figure 1.2a) and the proportion of aspen forests having coniferous recruitment (Figure 1.3) between the eastern and western extremes of the gradient, despite having contrasting fire regimes and climate. The higher total annual precipitation (Appendix A.1 – Figure A.1a) and the longer fire cycle (Appendix A.1 – Figure A.1c) in the east should, in principle, promote the aging of forests and an increase in shade-tolerant conifers (Lesieur *et al.*, 2002). Yet, only about a third of aspen stands examined (32 %) in QC contained conifer regeneration. This low proportion could be attributed to the intensification of forest management activities that have been undertaken in recent decades. Indeed, logging activity has increased in the southern boreal forest to the extent that it has become a major stand-replacing disturbance (Hart and Chen, 2008). In contrast, conifer recruitment was particularly low in the central part of the gradient (corresponding to MB and SK provinces) probably due to low annual precipitation (Appendix A.1 – Figure A.1a) and the aridity being higher (Appendix A.1 – Figure A.1b) in the region. Indeed, this portion of the gradient is usually characterized by a dry continental climate and a relatively short fire cycle (Appendix A.1 – Figure A.1c). Conifer recruitment is thus affected both by severe drought conditions that reduce the growth and survival of conifer seedlings and by the recurrence of severe fires, which leads to frequent rejuvenation of forest stands and promotes the establishment of pioneer species at the expense of late-successional species (Bergeron *et al.*, 2014). Fire affects both propagule availability and substrate suitability for

regeneration, which, in turn, impact regeneration and subsequent stand dynamics (Johnstone *et al.*, 2004; Johnstone and Chapin, 2006a). Mostly in the north, fire severity strongly affects the availability of regeneration microsites and, thus, has an important controlling influence on the density of initial conifer regeneration (Johnstone and Chapin, 2006a; Bergeron *et al.*, 2014). Whereas in the south, the pervasive presence of bluejoint grass, *Calamagrostis canadensis* (Michx.), in the aspen understory could be an additional limiting factor for coniferous regeneration, because of its adverse effects (competition) on the growth and survival of conifer seedlings (Landhäusser and Lieffers, 1998). In the Western Canada, the abundance of coniferous regeneration in aspen forests can be explained in part by the fact that the latitudinal gradient is very strong in this portion of the gradient, while boreal mixedwoods tend to occur further south when moving eastward (Figure 1.1). Obviously, the higher up north in boreal mixedwood, the closer you get to the coniferous forest.

The differences in conifer recruitment across Canada were most significant in terms of individual species. Among the major factors that guarantee the presence of a species in a forest landscape are favorable climatic conditions for its reproduction and growth, seed availability, the presence of suitable sites for its establishment and resilience to disturbances (Zasada *et al.*, 1992).

The abundance of Bf regeneration in the eastern portion of the gradient would be associated with a usually long return interval between fires and the maritime climate that characterizes this part of the Canadian boreal forest (Bergeron *et al.*, 1998). Conversely in aspen forests of western Canada, the recruitment of Bf would be limited because of the dry climate for germination and the fire size for seed dispersal. This species is more sensitive to drought than Ws (Messaoud *et al.*, 2007) and possesses large seeds compared to other conifer species, thereby limiting its potential for long-distance seed dispersal (Galipeau *et al.*, 1997). Bf regenerates primarily by

seed; its reproduction is severely limited by fire, because the presence of residual seed trees is required for site recolonization after disturbance (Galipeau *et al.*, 1997; Gauthier *et al.*, 2000). In regions that are affected by large fires in a cyclical manner (the case of the western Canada boreal forest), it is possible that Bf was gradually eliminated from the landscape over time (subsisting only in some small sectors naturally protected against fires), since this species is not fire-adapted. However, its native range extends towards western Canada in scattered stands through north-central Manitoba and Saskatchewan to the Peace River Valley in northwestern Alberta, then south for approximately 640 km (400 mi) to central Alberta and east and south to southern Manitoba (Frank, 1990).

Bs regeneration is still present in western aspen forests despite recurrent and severe fires in this portion of the gradient. This presence is facilitated by its adaptation to fire. It is generally able to re-establish itself quickly and amply after a fire event, as it has semi-serotinous cones that open under the effect of heat (Greene *et al.*, 1999; Lesieur *et al.*, 2002; Greene *et al.*, 2004). It is a transcontinental tree species across Canada (Frank, 1990).

The dominance of Ws regeneration in the aspen forests of western Canada seems contrary to the autecology of this coniferous species, given the predominance of short fire cycles (Appendix A.1 – Figure A.1c) and less favorable climatic conditions (low precipitation annual and drier) in this portion of the gradient. First, the abundance of Ws regeneration in western aspen stands could be explained by the greater availability of seeds of this species in this portion of the gradient. Indeed, Ws is ubiquitous in the forest landscapes of western Canada (Rowe, 1972). It is likely that the existing spatial patterns of the Ws, Bs and Bf regeneration abundance are a legacy of the regions' post-glacial history of vegetation. The overall distribution of conifer species is likely a consequence (biological legacy) of vegetation responses to environmental changes during the late Quaternary (Williams *et al.*, 2004). Interactive

maps of plant species distributions during the Holocene have been constructed from pollen diagrams, which reinforce this biogeographic hypothesis (NOAA, 2013). These maps indicate that during deglaciation, Ws began recolonizing the North American continent from the west, while Bf started in the east and Bs moved southward from refugia in the north. These species became adapted to their environmental conditions of the early periods of migration. The distribution of coniferous regeneration that is observed in aspen stands along the longitudinal gradient, therefore, could not be only interpreted as a response to pressure exercised by climate and disturbance regimes, but should actually reflect migration routes by which these species invaded the North American continent during the post-glacial period.

Ws regeneration is everywhere along the longitudinal gradient. The longevity, low mortality rate, periodic dispersion of large seed crops (i.e., masting) and shade-tolerance may explain the persistence of white spruce as a major species of the boreal forest (Gärtner *et al.*, 2011). White spruce regeneration, however, is very variable. Particularly in the west, this species seems to enjoy the absence of Bf and the low presence of Bs to increase in abundance. However, Ws is less dominant in eastern Canada, probably due to competition with Bf. Moreover, Ws is less shade-tolerant than Bf (Greene *et al.*, 2002).

Regarding the modeling of conifer recruitment across Canada, climate and anthropogenic proxies appear clearly as the determining factors. Despite its ecological impact on the regeneration of late-successional species (Johnstone and Chapin, 2006b), the fire regime (variable FC) did not appear in almost all of the selected predictive models. This is probably due to the fact that FC is very much correlated with DI ($r = 0.68$). Across Canada, the risk of forest fires is closely associated with drought severity and fire activity (Girardin *et al.*, 2004; Amiro *et al.*, 2005; Girardin *et al.*, 2008; Girardin and Wotton, 2009). Therefore, the inclusion of

DI in models masks the effect of fire, thereby rendering the variable FC non-significant. Temperature and soil moisture directly influence the success of conifer regeneration. Unfavorable weather conditions (e.g., drought) would compromise the processes of germination and establishment of conifer species (Williams *et al.*, 2004; Messaoud *et al.*, 2007; Martin-DeMoor *et al.*, 2010). Hydric stress or excessive temperatures during germination and seedling development can adversely affect their survival and incur significant mortality that is likely to limit or inhibit regeneration. For example, balsam fir seedlings in open spaces can undergo a high mortality rate when surface temperatures exceed 46 °C or when there is a drought or frost (Frank, 1990).

Furthermore, the variable "road density" (DensRoad25Km) mainly (or "distance to agricultural area" (DistAgri)) appears in almost all of the best models, with a negative effect on the abundance and occurrence of conifer recruitments. Increasing this variable suggests an increasing pressure from human activities and their impact on forest ecosystems. The consequences of this anthropization on forest characteristics are reflected in particular by increasing pressure timber harvesting due to population growth and fire occurrence following the introduction of new sources of ignition (risks of human-caused fires). These human actions lead to significant changes in the disturbance regime, with impacts ranging from local to global scales. Because tree species respond in different ways to changes in disturbance regime, alteration in fire regimes will affect forest composition. The cumulative effect of fires and forest harvesting usually favor early-successional species at the expense of late-successional tolerant conifers species. The recurrence of severe fires locally affects the seed bank of shade-tolerant species, which show a low dispersion capacity of seeds and a slow growth rate; unlike the shade-intolerant deciduous, which have traits better adapted to the new frequently disturbed environments (Boucher *et al.*, 2006a). Disturbances (fire and cut) occurring quite closely over time can therefore create local extinguishing pockets of shade-tolerant species, by accentuating the constraint of dispersion. The

decrease in coniferous species could be explained partly by the removal in large numbers of seed trees as a result of cuts (Archambault *et al.*, 1998). However, in a study aimed at describing and understanding the contribution of human activities to the transformations of forest landscapes since the early nineteenth century in the Bas-Saint-Laurent in eastern Quebec (Terrial *et al.*, 2013), researchers observed a dramatic increase in the absolute and relative frequency of deciduous species. This increase was accompanied by a decrease in coniferous trees that dominated pre-industrial forests, such as spruce (Picea spp.) and cedar (Thuja occidentalis L); only balsam fir seems more resistant. Human activities were a major factor in this dominance of deciduous species.

In addition to logging, forest clearing for farmland in the north-east of North America was accompanied by bush fires, which escaped in the surrounding forests. The study findings showed that 90 % of the fire surface is less than 2 km from colonization zones. These results imply a strong connectivity between fires and colonization compared to a random distribution of fires, an indication of the importance of anthropogenic fires in landscapes. The current location of aspen stands seems to match the fire occurrence of colonization in this region.

1.6 Conclusion

Our study shows that coniferous regeneration is present in aspen stands across an east-west transect of Canada, with the exception of stands that are affected by human activities. Conifer regeneration is persistent despite the observed variability in climate and disturbance regimes along this transect. However, the spatial pattern of abundance and the occurrence of conifer regeneration varied differently depending on the species. Within the context of global warming, a future increase in the risk and severity of fires could lead to changes in the current dynamics of conifer species recruitment in these types of stands. An increase in temperature and drought and,

consequently, in fire activity would significantly limit the natural regeneration of balsam fir in aspen forests across boreal landscapes. Given that black spruce is particularly well adapted to fire, the distribution of its natural regeneration in boreal mixedwood could be less affected by climate change impacts. White spruce showed a certain degree of plasticity in its response to environmental variation. It grows in widely varied environments, including regions characterized by less favorable climate and soils. Given that silvicultural management could lead to an increase in deciduous cover, the results of this study provide some insights into how boreal forest composition could be affected by future climate change..

1.7 Acknowledements

We are very grateful to the various provincial forest branch managers (Québec, Ontario, Manitoba, Saskatchewan, Alberta and British-Columbia) for making their forest inventory data available to us. We especially would like to thank Yassine Messaoud (former Postdoctoral researcher., Faculty of Forestry and the Forest Environment, Lakehead University) and Dave Gervais (former Professional Chair AFD-UQAM-UQAT) for their support in data acquisition, Remi St-Amant (NRC), who provided us with the climatic data, and the research professionals of the Centre d'Étude de la Forêt (Daniel Lesieur, Mélanie Desrochers and Marc J. Mazerolle for technical assistance; and William F.J. Parsons for the English revision).

Figure 1.1 Map of the study area, along an east-west transect in Canada. The light grey area represents the "boreal mixedwood" ecoregion of Canada (Source: Baldwin et al. 2012). Black spots represent our study sites.

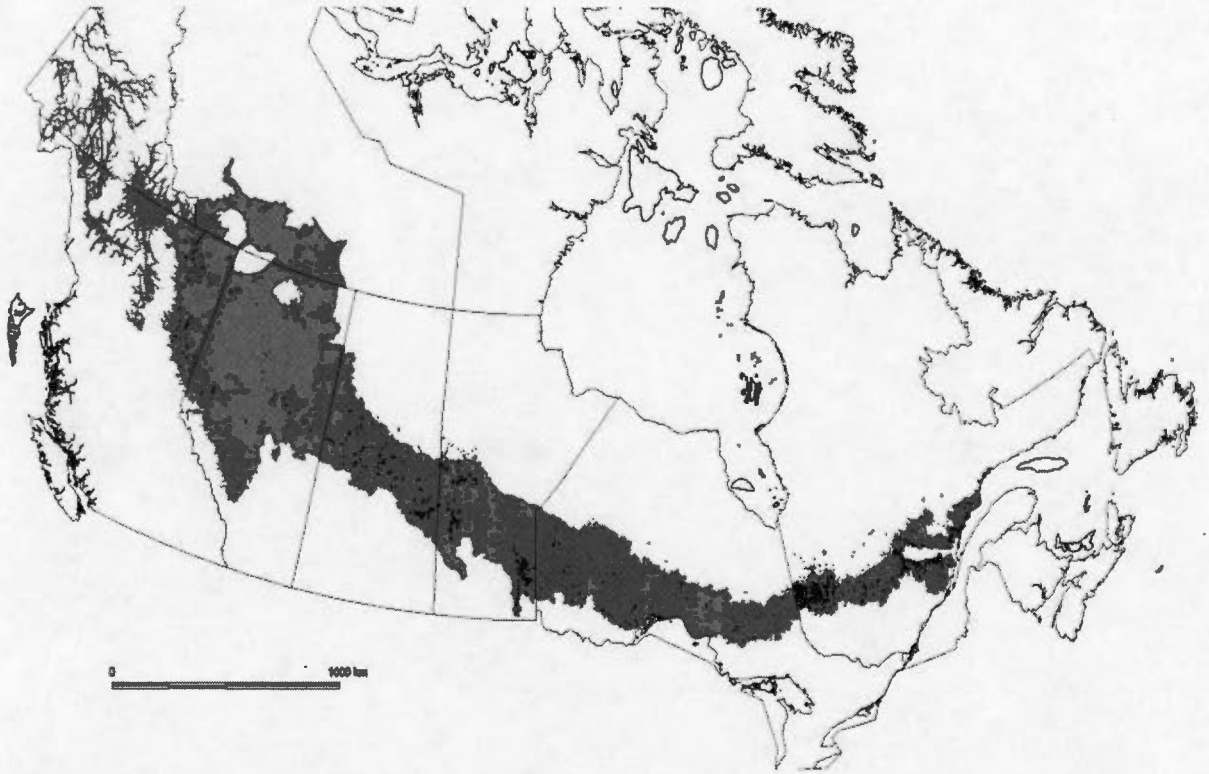


Figure 1.2 Density distribution of coniferous regeneration (Conif), along the east-west gradient in Canada. Bf, balsam fir; Bs, black spruce; Ws, white spruce. Longitudinal coordinates of each stand were rounded up to the immediately above whole value (i.e., longitude = 2 × ROUNDED (true longitude/2; 0)) to simplify the presentation of results, given the large number of observations (n = 2636). Point clouds represent the averages of abundance per hectare for the three species combined (a) Conif: squares; balsam fir (b) Bf: triangles; black spruce (c) Bs: circles; and white spruce (d) Ws: diamonds. In each graph, the trend of variation in abundance along the longitudinal axis is represented by a linear regression (red line).

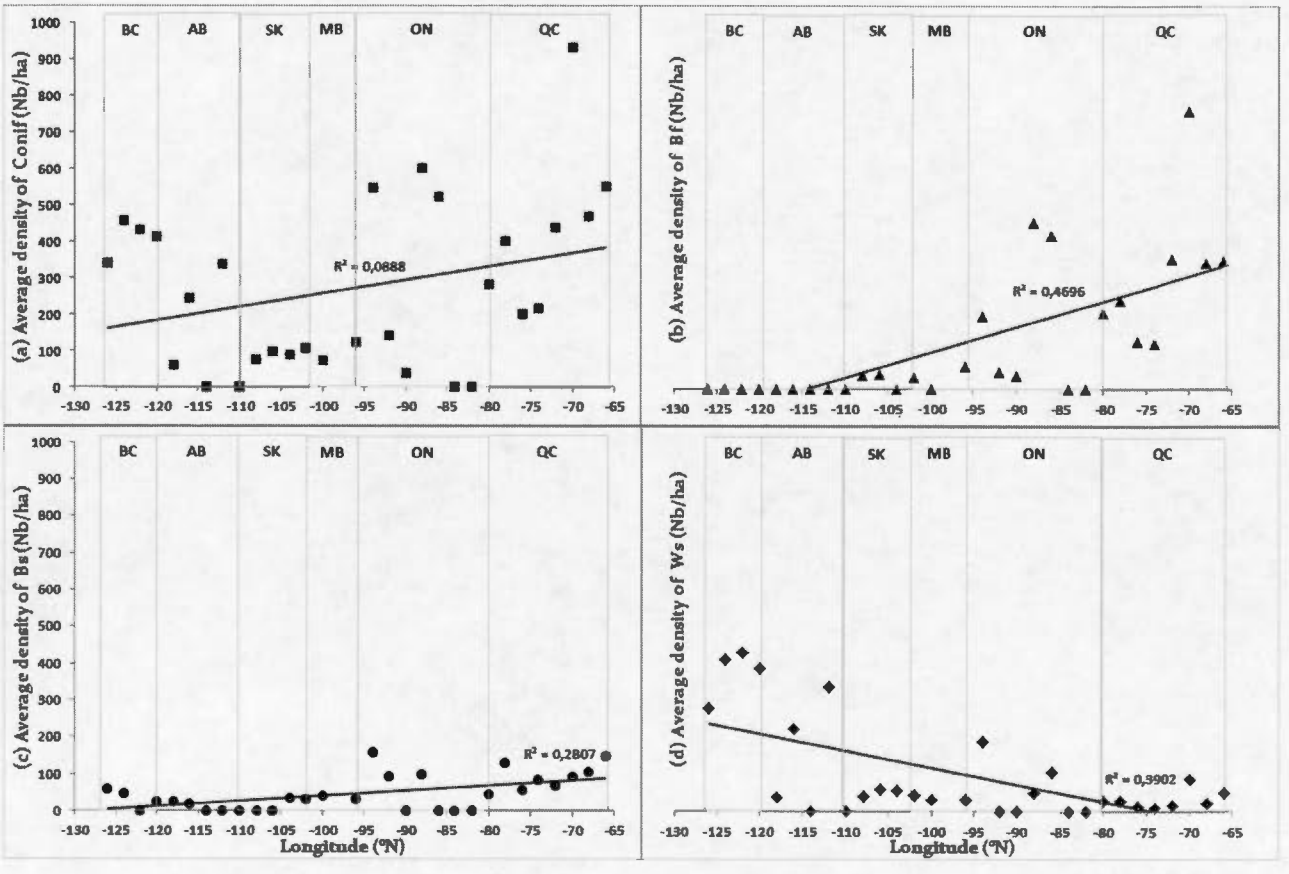


Figure 1.3 Frequency of occurrence (%) of aspen stands with conifer regeneration. Frequency of occurrence is the ratio of the number of aspen stands with at least one sapling of a coniferous species over the total number of aspen stands examined in a province (in percent). In the graph above, the histograms are the frequencies for all three species combined (Conif), white spruce (Ws), black spruce (Bs) and balsam fir (Bf) respectively.

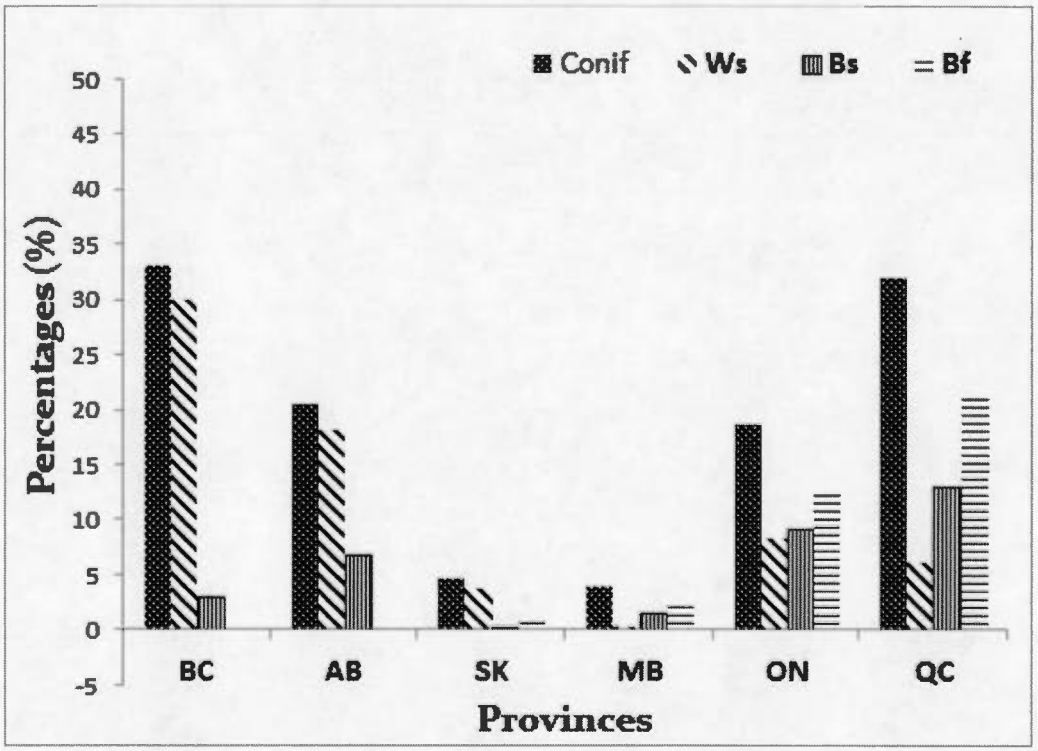


Table 1.1 Summary of trembling aspen study stands (by Canadian province) with longitudinal and latitudinal ranges and average site characteristics.

Provinces[a]	No. of stands[b]	Longitude (W)	Latitude (N)	T° mean (°C)[c]	Total Precipitation (mm)[c]	Relative Humidity (%)[c]	Drought index (mm)[c]	Fire cycle (years)[c]
BC	100	120°04'–125°06'	55°11'–59°88'	0.8 (–1.3 – 2.9)	504 (449 – 573)	57 (53.6–60)	97 (57.2–136.2)	387.4 (326.8–397.9)
AB	44	111°01'–119°43'	51°86'–58°58'	1.8 (–0.7 – 2.8)	490 (415 – 560)	54.4 (49.2–59.8)	100.4 (69.7–126.7)	332.7 (93–672.9)
SK	470	101°75'–109°80'	52°33'–55°72'	0.9 (–0.3 – 1.4)	461 (399 – 536)	55.2 (50.8–60.4)	107.7 (81–132.8)	301.9 (50.9–1225.6)
MB	574	95°27'–101°92'	49°15'–55°36'	1.5 (–1.3 – 3.2)	532 (445 – 657)	57.3 (52.7–62.6)	95.3 (72–129.9)	325.7 (56.2–1225.6)
ON	155	79°85'–95°1'	47°5'–52°58'	1.6 (–0.4 – 2.7)	736 (610 – 881)	56.8 (52.5–61)	51.1 (27.1–72.7)	748.3 (83.9–1440.2)
QC	1293	66°98'–79°51'	47°54'–50°36'	1.4 (–0.7 – 3.7)	931 (841 – 1256)	55.8 (50.7–67.8)	28 (10.4–64.5)	1360.5 (625.7–3706.6)
Total or ranges	2636	66°98' – '125°06'	47°5' – 59°88'	–1.3 – 3.7	399 – 1256	49.2 – 67.8	10.4–136.2	50.9–3706.6

[a] BC (British Columbia), AB (Alberta), SK (Saskatchewan), MB (Manitoba), ON (Ontario) and QC (Quebec); [b] The total number of aspen stands selected by province in Canada; [c] Values in parentheses are ranges.

Table 1.2 Types and description of predictive variables used in the models.

Variable (abbreviation)	Type	Description	Data source
		Climatic	
Drought index (DI)	Continuous (class)	Annual mean aridity (1981-2010) (mm)	Environment Canada 2013
Degree-days (DD)	Continuous (class)	Annual mean degree-day over 5°C (1981-2010) (°C day)	Environment Canada 2013
		Fire regime	
Fire Cycle (FC)	Continuous (class)	Year interval from cyclic return fire (Years)	Boulanger *et al.* 2012
		Physical environment	
Distance to the nearest great river, lake or bay (DistWater)++	Continuous (class)	Distance to the nearest significant watercourse (Km)	Natural resources of Canada - Geobase
Hydrography (PctHydro)	Continuous (class)	Percentage of area occuped by water in a radius of 15 Km around the stand (%)	Natural resources of Canada - Geobase
Physiographic regions (RegiPhysio)	Character	Three major regions of the physical geography of the Canadian landscape: Canadian Shield, Interior Plains and Western Cordillera	Atlas of Canada
		Anthropogenic	
Distance to the nearest main road (DistRoad)	Continuous (class)	Distance to the nearest carriage road (Km)	Natural resources of Canada - Geobase
Distance to agricultural area (DistAgri)	Continuous (class)	Distance to the nearest farmland (Km)	Natural resources of Canada - Geobase
Road density (DensRoad)	Continuous (class)	Total length of roads (Km) / Km2 area, in a radius of 15 and 25 Km around the stand	Natural resources of Canada - Geobase
		Spatial	
Longitude (Long)	Continuous	Geographic coordinates	Database forest inventory
Latitude (Lat)	Continuous	Geographic coordinates	Database forest inventory
Elevation (Elev)	Continuous	Geographic coordinates	Database forest inventory

++ The size of the watercourse considered in the analysis ranged from 5 to 35,000 km^2 (an average of about 340 km^2).

Table 1.3 Description and best models of abundance, based on Akaike's information criterion (AIC).

Response	Candidate models	Model ID	LogLik	AIC	ΔAIC	W_i
Conif	**DI + DensRoad25Km + Lat**	**mod1**	**-22158**	**44325**	**0.0**	**0.61**
	DI + DensRoad25Km + DD	mod2	-22158	44327	1.5	0.29
	DI + DensRoad25Km	mod3	-22160	44329	3.5	0.11
	DI	mod4	-22169	44344	19.2	0.00
	RegPhysio+DensRoad25Km+FC +DistAgri	mod5	-22175	44364	39.1	0.00
	FC+DensRoad25Km+Lat	mod6	-22186	44381	56.1	0.00
	DD+DensRoad25Km+FC+Elev	mod7	-22185	44382	56.4	0.00
	DD + DensRoad25Km +FC	mod8	-22192	44393	68.0	0.00
Ws	**DD+DensRoad25Km+Lat**	**mod1**	**-17922**	**35855**	**0.0**	**0.88**
	DD+DensRoad25Km+Long	mod2	-17925	35860	4.5	0.09
	DI+DistRoad+Lat	mod3	-17927	35862	6.8	0.03
	DD+DensRoad25Km	mod4	-17930	35869	13.9	0.00
	DD+Long+Lat	mod5	-17932	35873	18.1	0.00
	DI+DistRoad+Long	mod6	-17932	35875	19.6	0.00
	DD+Long	mod7	-17937	35883	27.9	0.00
	DI+Long	mod8	-17937	35883	28.0	0.00
Bs	**DI+DensRoad25Km+Lat**	**mod1**	**-19065**	**38140**	**0.0**	**0.39**
	DI+DensRoad25Km+Long	mod2	-19066	38141	0.8	0.26
	DI+FC+DensRoad25Km	mod3	-19066	38141	1.1	0.23
	DI+DensRoad25Km	mod4	-19067	38142	2.3	0.12
	DI	mod5	-19081	38169	28.4	0.00
	DD+FC+DensRoad25Km+Elev	mod6	-19081	38174	33.6	0.00
	DD+FC+DensRoad25Km	mod7	-19084	38178	37.8	0.00
	FC+DensRoad25Km	mod8	-19087	38181	40.7	0.00
Bf	**DI**	**mod1**	**-21874**	**43754**	**0.0**	**0.99**
	RegiPhysio+FC+DistWater	mod2	-21880	43773	19.0	0.00
	FC+DD+RegiPhysio	mod3	-21881	43774	19.8	0.00
	FC+RegiPhysio	mod4	-21884	43778	24.1	0.00
	FC+DistWater	mod5	-21898	43805	51.0	0.00
	FC+DD	mod6	-21899	43807	52.7	0.00
	FC	mod7	-21901	43808	54.3	0.00

Note. logLik is the log-likelihood value of the model; AIC is the Akaike information criterion value; ΔAIC is the delta AIC, a measure of each model relative to the best model; and wi is the Akaike weights, representing the ratio of the ΔAIC of a given model relative to the whole set of R candidate models; Conif, Ws, Bs and Bf refer to the conifer recruitment into aspen stands across Canada, respectively, for all three conifer species combined, white spruce, black spruce and balsam fir; models are ranked based on their AIC scores, where the smallest AIC represents the best model (in bold).

Table 1.4 Summary of the multiple regression for Abundance (variables significant at $p < 0.05$).

Response	Parameters	Estimate	Lower 95% CI	Upper 95% CI	SE	t value	Pr(>|t|)
Conif	DI	-131.7	-165.25	-98.33	17.07	-7.72	0.00
	DensRoad25Km	-123.4	-187.40	-59.44	32.63	-3.78	0.00
	Lat	33.4	5.42	61.42	14.28	2.34	0.02
Ws	DD	-24.8	-35.49	-14.19	5.433	-4.57	0.00
	DensRoad25Km	-31.5	-44.37	-18.65	6.559	-4.81	0.00
	Lat	6.3	3.22	9.45	1.588	3.99	0.00
Bs	DI	-29.9	-40.25	-19.55	5.280	-5.66	0.00
	DensRoad25Km	-49.5	-69.36	-29.77	10.095	-4.91	0.00
	Lat	9.1	0.50	17.83	4.418	2.07	0.03
Bf	DI	-77.2	-93.69	-60.74	8.403	-9.19	0.00

Based on the t-test, the table shows the significance for each variable included in the best model individually (Table 1.3); SE, standard error; CI, confidence interval.

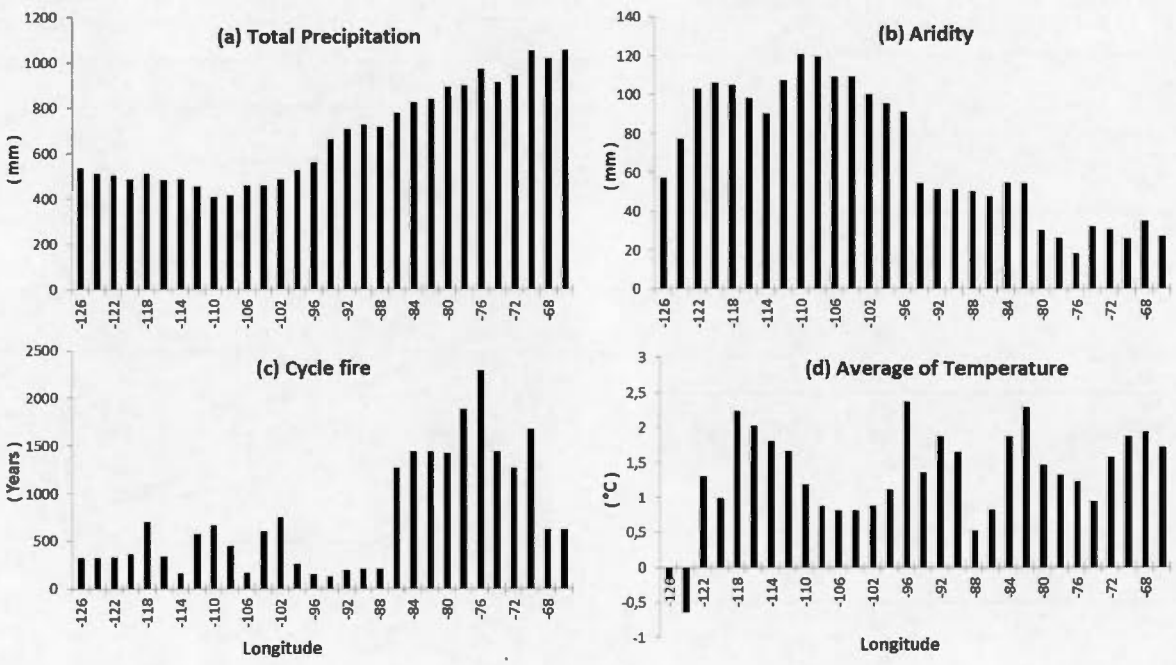
Table 1.5 Variance proportion of predictive variables for the abundance.

Model	Predictors	Variance (%)
Conif	DI	45.8
	DensRoad25Km	11.1
	Lat	4.3
Ws	DensRoad25Km	29.4
	DD	26.6
	Lat	20.3
Bs	DI	39.8
	DensRoad25Km	29.3
	Lat	3.1
Bf	DI	‡

‡: no data. DI is the only one variable in the Bf model for the abundance.

APPENDICE A.1.

Figure A.1 Histograms illustrating the variability of environmental conditions (averages of last 3 decades) based on the longitudinal gradient for total annual precipitation, drought index (aridity), cycle fire, and average annual temperature. The linear regression on each histogram indicates the trend of fluctuations in the distribution of the variable across the study gradient



APPENDICE A.2.

Table A.1 Description and best models of occurrence based on Akaike's information criterion (AIC).

Response	Candidate models	Model ID	logLik	AIC	ΔAIC	W_i
Conif	**DistAgri+DI+Lat+RegiPhysio+Long+Elev+DD+PctHydro**	**mod1**	**-1111**	**2240**	**0.0**	**0.98**
	DistAgri+DI+Lat+RegiPhysio+Long+Elev	mod2	-1117	2248	8.3	0.02
	DistAgri+DI+Lat+RegiPhysio+Long	mod3	-1123	2257	17.2	0.00
	DistAgri+DI+PctHydro+Lat+RegiPhysio+DD	mod4	-1132	2278	38.1	0.00
	DistAgri+DensRoad25Km+DI+PctHydro+Lat	mod5	-1136	2283	43.2	0.00
	DistAgri+DensRoad25Km+DI+DD	mod6	-1147	2304	63.9	0.00
	DistAgri+DensRoad25Km+DI	mod7	-1157	2321	81.1	0.00
	DistAgri+RegiPhysio+CF+DensRoad25Km	mod8	-1198	2406	165.8	0.00
Ws	**DensRoad25Km+DI+Lat+Long+Elev+DD**	**mod1**	**-506**	**1026**	**0.0**	**0.88**
	DensRoad25Km+DI+Lat+Long+Elev	mod2	-509	1030	3.9	0.12
	PctHydro+DensRoad25Km+DI+Lat+Long	mod3	-519	1049	23.1	0.00
	PctHydro+DensRoad25Km+DI+Lat+DistAgri	mod4	-519	1051	24.5	0.00
	PctHydro+DensRoad25Km+DI+Lat	mod5	-523	1055	28.7	0.00
	DD+DistAgri+PctHydro+DensRoad25Km+Long+DI	mod6	-525	1065	38.5	0.00
	DD+DistAgri+PctHydro+DensRoad25Km	mod7	-534	1079	52.4	0.00
	DI+DD+CF	mod8	-541	1090	64.0	0.00
Bs	**DistAgri+DensRoad25Km+DI+Lat+Long+RegiPhysio**	**mod1**	**-585**	**1184**	**0.0**	**0.39**
	DistAgri+DI+Lat+Long+RegiPhysio+DistRoad	mod2	-585	1184	0.2	0.35
	DistAgri+DensRoad25Km+DI+Lat+Long	mod3	-587	1185	0.9	0.25
	DI+DD+CF+DistAgri+DensRoad25Km	mod4	-591	1195	10.5	0.00
	DensRoad25Km+DI+Lat+Long	mod5	-593	1196	11.9	0.00
	DistAgri+DensRoad25Km+DI+Lat+Long+RegiPhysio	mod6	-593	1197	12.7	0.00
	DI+DD+CF+DistAgri	mod7	-595	1200	15.8	0.00
	DI+DD+CF	mod8	-602	1212	28.3	0.00
Bf	**RegiPhysio+PctHydro+DistAgri+DI+Long+CF**	**mod1**	**-767**	**1548**	**0.0**	**0.87**
	RegiPhysio+PctHydro+DistAgri+DI+Long	mod2	-770	1552	3.8	0.13

RegiPhysio+DistAgri+DI+Long+CF	mod3	-775	1563	14.7	0.00
DistAgri+DI+Long+CF	mod4	-781	1572	23.8	0.00
RegiPhysio+PctHydro+DensRoad15Km+DistAgri+DI	mod5	-783	1578	30	0.00
RegiPhysio+PctHydro+DensRoad15Km+CF+DistAgri	mod6	-799	1611	62.6	0.00
RegiPhysio+PctHydro+DensRoad15Km+CF	mod7	-803	1615	67.2	0.00

Note: LogLik is the log-likelihood value of the model; AIC is the Akaike information criterion value; ΔAIC is the delta AIC: a measure of each model relative to the best model; and W_i is the Akaike weights: represent the ratio of the ΔAIC of a given model relative to the whole set of R candidate models. Conif, Ws, Bs and Bf refers to the conifer recruitment into aspen stands across in Canada respectively for all three conifer species, white spruce, black spruce and balsam fir, Models are ranked based on their AIC scores where the smallest AIC represents the best model (in bold).

CHAPITRE II

CLIMATE AND DISTURBANCE REGIME EFFECTS ON ASPEN (*Populus tremuloides* Michx.) STAND STRUCTURE AND COMPOSITION ALONG AN EAST-WEST TRANSECT IN CANADA'S BOREAL FOREST.

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2.1 Abstract

Stand structure and composition play a key role in maintaining the ecological integrity of the boreal forest. However, future changes in climate and disturbance regime could affect these forest attributes. Using provincial forest inventory datasets, we analyzed stands dominated by aspen (≥ 75% of the plot total basal area) distributed along a wide longitudinal gradient of environmental conditions across Canada. Stands were classified into three diameter structure types (inverted J, intermediate, and advanced). There was no major difference in the distribution pattern of structural types of aspen-dominated stands between the western and eastern Canadian boreal mixedwood forests, despite a marked contrast in climatic conditions and fire regime. These results suggest that the predominance of juvenile structures in the western aspen forests is mainly related to the frequent recurrence of fires, while within eastern aspen forests, the longer fire cycle was not the controlling factor of stand structure. Anthropogenic activities would have strongly shaped the structure of aspen forests in eastern Canada. White spruce in the west and balsam fir in the east are among the main shade-tolerant conifer companion species associated with these stands. Although stand structure and composition were highly related to stand age and site productivity, regional climate and human activities, through their influence on disturbance regime, might have impacted these forest attributes.

Key words: climate, disturbances regime, stand structure and composition, aspen (*Populus tremuloides*), even and uneven-sized stand, boreal mixedwood forest.

Résumé

La structure et la composition des peuplements figurent parmi les caractéristiques clés pour le maintien de l'intégrité écologique de la forêt boréale. Cependant, les changements climatiques en cours et leurs effets sur les régimes de perturbation pourraient affecter ces attributs forestiers d'intérêt. A l'aide des données d'inventaires

forestiers provinciaux, nous avons analysé les peuplements dominés par le tremble (≥ 75% de surface terrière totale en tremble) repartis le long d'un large gradient longitudinal de conditions environnementales à travers le Canada. Les peuplements de l'étude étaient classés dans trois types de structure diamétrale (J inversé, Intermediaire et avancé). Il n'y avait pas de différence majeure dans le patron de distribution de types structuraux entre les peuplements de tremble dans l'Ouest et ceux dans l'Est de la forêt boréale mixte du Canada, en dépit du contraste marqué dans les conditions climatiques et les régimes de feux. Ces résultats suggèrent que la prédominance de structures juvéniles dans les tremblaies de l'ouest est principalement reliée à la récurrence fréquente des incendies; tandis que dans les tremblaies de l'est, le cycle de feu plus long n'a pas été le facteur déterminant de la structure du peuplement. Les activités anthropiques auraient fortement façonné la structure des tremblaies dans l'est du Canada. L'épinette blanche dans l'ouest et le sapin baumier dans l'Est sont parmi les principales espèces compagnes de conifères tolérants à l'ombre associées avec ces peuplements. Bien que la structure et la composition de peuplements étaient fortement corrélées avec l'âge du peuplement et la productivité du site, le climat régional et les activités humaines, grâce à leur influence sur le régime des perturbations, pourraient avoir impacté ces attributs forestiers.

Mots-clefs: climat, régimes de perturbations, structure et composition du peuplement, tremble (*Populus tremuloides*), distribution diamétrale équienne et inéquienne, forêt boréale mixte.

2.2 *Introduction*

Stand structure and composition are important characteristics for maintaining the ecological integrity of forest ecosystems (Kuuluvainen, 2002). In the boreal forest, complex interactions involving biotic and abiotic components of the ecosystem drive these characteristics, as well as their evolution over time (Bergeron *et al.*, 2014). Within forested areas, different types of stand structure is found in various proportions from one area to another, depending on the dominant tree species in the canopy, environmental conditions, and associated disturbance regimes (Chen and Popadiouk, 2002; Shorohova *et al.*, 2009). For example, regions subjected to short fire cycles tend to develop a majority of young forest stands, which generally exhibit a regular and even-sized structure. Conversely, in regions subjected to longer fire cycles (around 200 years and over), old, irregular and uneven-sized stands predominate (Boucher *et al.*, 2003). In the prolonged absence of severe fires, secondary disturbances (e.g. insect outbreaks and other stand-level processes such as windthrow of low severity) promote the development of irregular structures (Kneeshaw and Bergeron, 1998; McCarthy, 2001). In recent decades, anthropogenic activities such as forest harvesting and silviculture were additionally considered as major disturbances likely to affect forest structure and composition at both the stand and landscape scales (Boucher *et al.*, 2006a; Boucher *et al.*, 2009).

Future climate projections predict changes in temperature and precipitation regime, which could lead to substantial changes in the structure and functioning of ecosystems, including species composition and distribution (IPCC, 2007). Temperature increases are expected to be particularly pronounced at northern latitudes (Field *et al.*, 2007; IPCC, 2007), which could induce regional-specific alterations in the fire regime, leading to uncertain but potentially significant impacts on ecosystem components in the boreal zone of Canada (Gauthier *et al.*, 2014). Changes in climate, and by extension the natural disturbance regime, will affect not only the composition and structure of forest stands, but also the rate at which the

changes of these occur. Chen *et al.* (2009) argue that if there is an increase in fire occurrence due to climate change, the boreal landscape will become dominated by early-successional stands mostly composed of hardwoods and mixtures of hardwoods and conifers. The mixed-species stands are arguably more structurally diverse than their single-species counterparts, due notably to inherent differences in growth rates among tree species (Varga *et al.*, 2005). A better understanding of factors affecting forest characteristics, and the relative importance of different spatial patterns of these characteristics across boreal regions offers promising perspectives for implementing a sustainable management approach to preserve the ecological integrity of forest ecosystems.

This study focuses on stands dominated by aspen (*Populus tremuloides* Michaux), and aims to (*i*) characterize the structure and composition of these stands, and to estimate how their abundance changes along an East-West transect across the Canadian boreal forest; and (*ii*) analyze the variability observed in these stands along this transect, based on eco-environmental factors. Aspen is the most abundant deciduous tree species in North America (Perala, 1990) and has a transcontinental distribution in Canada, where its ecological and economic contribution has increased in recent decades (Peterson and Peterson, 1992). This pioneer species is relatively short-lived, reaching the age of senescence around 100 years (Cumming *et al.*, 2000). During the process of senescence of the first cohort, a second cohort of aspen as well as coniferous species can grow and emerge in the canopy to form a mixed stand (Chen and Popadiouk, 2002), depending upon the rate at which the aspen stand is invaded by coniferous species (Bergeron, 2000).

The analysis of vegetation dominated by the same canopy species across a wide and continuous forest ecosystem would help to better understand the response of this vegetation in a changing environment. So, the pan-Canadian scope of this study on aspen is quite exceptional in North America. There are large regional variations in

climatic factors and fire regime among and within the Canadian regions (Stocks *et al.*, 2002; Bergeron *et al.*, 2004; Boulanger *et al.*, 2012). In most boreal regions of eastern Canada, the fire interval often exceeds the longevity of tree species (Kneeshaw and Gauthier, 2003). In contrast, the shorter fire cycles in the western boreal forest result in a forest matrix dominated by young post-fire stands with patches of older forests dispersed throughout (Johnson, 1996). Based on the regional differences outlined above, we hypothesize that (*a*) young, even-sized aspen-dominated stands will be more frequent in western Canada, whereas old, uneven-sized aspen-dominated stands will be more frequent in eastern Canada; and (*b*) pure aspen stands will be more abundant in western Canada due to shorter fire cycles, that would limit changes in canopy composition. Conversely, longer fire cycles in eastern Canada would tend to increase the proportion of aspen stands with an understorey of shade-tolerant tree species.

2.3 Methods

2.3.1 Study area and data selection

The study was located in the boreal mixedwood ecological zone of Canada (Fig. 2.1), using the forest inventory databases available in the different provinces. This forest zone is influenced by a wide range (from east to west) of factors including climate, edaphic conditions, disturbance regimes, and management histories (Bergeron *et al.* 2014). It is characterized by a complex mosaic of forest types that vary both structurally and in the relative proportion of broadleaf and conifer tree species (Bergeron *et al.*, 2014). Although this forest zone is dominated by mixed species stands, many pure deciduous stands were found in the early-successional stages (Bergeron *et al.*, 2014). Studied stands are spread throughout an uninterrupted transcontinental band that extends from British Columbia in the west to Quebec in the

east (Fig. 2.1), and whose stand and environmental characteristics are summarized in Table 2.1.

Data selection was carried out in several steps, as detailed in Nlungu-Kweta *et al.* (2014). We first selected forest stands from the provincial forest inventory datasets that were dominated by aspen, *i.e.*, at least 75% of the basal area ($m^2.ha^{-1}$) of live and merchantable trees [diameter at breast height (DBH) ≥ 9 cm] located in all temporary sample plots (TSPs), and in only one set of inventory measures (the most recent available) of permanent sample plots (PSPs) comprised of aspen. The threshold of at least 75% of plot total basal area in aspen was chosen to ensure that stands originated from a stand-replacing disturbance. Then of the preselected stands, we retained only those that were located within the study area by using ArcGIS 9. Overall, 2582 stands dominated by aspen were selected for this study (Table 2.1)[1].

2.3.2 Characterisation of aspen-dominated stands along the study transect

Stands were characterized based on a range of different structural and compositional typologies. All living trees with a DBH ≥ 9 cm in the plot were used to describe stand structure and composition. As the survey areas of trees included in the study differed in size among the Canadian provinces, data from the selected sample plots had to be harmonized before stand characterisation. This was accomplished by taking the stem density observed in each plot, and extrapolating the said density at the scale of a larger forest (one hectare).

2.3.3 Typological classification of stand structure and composition

The classification of the studied stands into structural types was carried out by combining the relative distributions of density ($trees.ha^{-1}$) and basal area ($m^2.ha^{-1}$) per

[1] We added a table (Appendice B.1) showing the distribution of aspen stands [mixed and aspen-dominated stands, respectively having ≥ 50 % and ≥ 75 % of total basal area in aspen] per province, in the study area.

DBH class (in the stand) - an approach developed in British Columbia by Moss (2012), who used stand structure classes to predict ecological succession pathways. DBH data were compiled into 14 classes, as follows: 2-cm diameter classes between DBHs of 9-28 cm, 4-cm diameter classes between DBHs of 29-40 cm, and DBH > 40 cm class. Class limits were determined arbitrarily and refer to the dimensions generally used in silviculture for merchantable stems. In order to adjust the data to a minimum resolution of 400 m^2 (the size of the smallest sampling unit of trees that was common among all studied provinces), we excluded stems of diameter classes where the density was less than 25 trees.ha^{-1} (1 tree/400 m^2 = 25 trees.ha^{-1}) during the stand structural classification process. Following exploratory tests on the optimal number of clusters, stands were automatically classified into one of three main structural types, using the K-means clustering method (Borcard *et al.*, 2011) under R 3.1.2 (R Development Core Team, 2013). This clustering method considered the cumulative distributions of tree diameter classes.

However, to determine if the spatial tree distribution per DBH class in the stand was regular or irregular (even- and uneven-sized stand structures, respectively), the autocorrelation function (Legendre and Legendre, 2012) was used as a supplementary "structural index". For this purpose, the autocorrelation in the diameter class distributions was estimated by computing the Pearson correlation coefficient (r) between observed densities per diameter class and their lags at a distance of 1 shift (lag of order 1). Even- and uneven-sized stand structures were identified by using the critical value for the first-order autocorrelation (ρ_1) at $P < 0.05$ derived from standard tables. When $r > \rho_1$, the tree distribution was monotonic or unimodal Gaussian; and when $r < \rho_1$, the distribution was random and irregular, in which trees belonged to several diameter classes. We then analyzed the relationship between the observed structural types, stand age and site productivity.

Compositional classification was used to categorize the studied stands among three compositional types, depending on the percentage of basal area ($m^2.ha^{-1}$) of aspen. A detection threshold for the "presence" of a tree species was set at 25 individuals (trees) per hectare, corresponding to the minimum density of trees for a given species in 400 m^2 (the aforementioned minimum resolution). Thus, to standardize information acquired under different sampling protocols, a tree species was excluded from the compositional stand analysis when its density fell below 25 $trees.ha^{-1}$. Depending on the dominance of aspen in a stand, we distinguished: (*i*) "pure-aspen stands" to designate those with 100 % basal area made up of aspen; (*ii*) "almost pure-aspen stands" where aspen represents 90-99.9 % of basal area; and (*iii*) "least pure-aspen stands" where aspen represents 75-89.9 % of basal area. In the "least pure-aspen stands" category, we then identified the main companion tree species in the stand, i.e., tree species with commercial value that had the next highest basal area following aspen.

To illustrate the relative distribution of various structural and compositional types at the landscape level along the longitudinal gradient, we quantified their respective frequencies (expressed as %) within the studied provinces. This was done by calculating the ratio between the number of aspen stands with a given structural or compositional type and the total number of aspen stands examined in a province. Pearson's Chi-squared test was performed to test for significant differences in the structural and compositional frequencies among provinces.

2.3.4 Predictive variables for modelling structural types

The modelling effort was focused solely on stand structure; here, the study challenge was not about the compositional types mentioned above but rather whether species composition had an effect on stand structure. To identify factors influencing stand structure, and predict structural types of aspen-dominated stands across the Canadian boreal mixedwood forest, sixteen potential predictor variables (k = 16) were tested.

Their sources and descriptions are summarized in Table 2.2. These are: Tree species richness (RichSp), as the diversity of tree species would imply a variability in tree size (Lähde *et al.*, 1999); Stand age (Age), as the stand structure changes over time; Site productivity, expressed by site index (SI) - which may affect the maturation rate of trees within a stand; Interaction between stand age and site productivity (Age*SI) - since the age effect may be altered by site productivity; Climatic conditions of sites, expressed both by the aridity index (AI) which is the accumulated monthly water deficit and the cumulative degree-days above 5°C (DD); Fire cycle (FC), to characterize the fire regime of sites; Nearest distances to various landscape features were estimated in ArcGIS and included major watercourses (DistWater; rivers, lakes and bays), main road (DistRoad) and agricultural area (DistAgri); Percentage of hydrography (PctHydro); road density (DensRoad); and spatial variables (longitude, latitude and elevation).

Several applicable site index models exist across the provinces covered by this study, however, we have chosen to use the model of Nigh *et al.* (2002) to estimate site index because it produced the best fit for the transect data (Anyomi *et al.*, 2015)[2]. Since climate is a complex process that affects tree growth, a 30-year average of DI and DD was generated in BioSIM 9 (Régnière and Saint-Amant, 2008) using Environment Canada data (Environment Canada, 2013).

Fire is the most important stand-replacing disturbance agent in the boreal forest (Johnson, 1996), and stand structure is largely a reflection of the time elapsed since the last stand-replacing disturbance event. FC data was obtained using a map that defines areas with a homogeneous fire regime. Secondary disturbances, mainly forest

[2] A research note is in preparation, entitled "Portability of site index models for boreal aspen stands of Canada" (Anyomi *et al.* 2016), justifying the choice of the model of Nigh *et al.* (2002) compared to four other competitor models [Pothier and Savard (1998); Plonski (1956); Huang *et al.* (2009); and Garcia (2013)].

tent caterpillar (*Malacosoma disstrium* Hübner) outbreak, were not included in the modeling effort due to a lack of data at the pan-Canadian scale.

DistRoad and DistAgri, as well as DensRoad15km and DensRoad25km, were estimated and considered as proxies to investigate potential anthropogenic influences on the natural environment. Anthropogenic disturbances can alter landscape dynamics, by acting at similar scales to natural disturbances (Laquerre *et al.*, 2009), particularly through fire occurrence (increased ignition sources). Changes in fire regime due to forest management practices such as harvesting have a direct impact on the composition and structure of forests (Bergeron *et al.*, 2004; Bergeron *et al.*, 2001). DistWater and PctHydro were added as variables describing the physical environment of sites. An abundance of water (PctHydro) can create micro-climatic conditions that affect surrounding areas, while major rivers can act as natural barriers against forest fires.

Within the North American boreal forest, climatic factors vary according to changes in spatial gradients (Hart and Chen, 2006); hence we also included longitude, latitude and elevation as climatic surrogates in the analysis.

2.3.5 Model Selection and logistic regression

A model selection approach based on Akaike's Information Criterion (AIC) (Mazerolle, 2006) was used to identify which among all of the eco-environmental variables cited in Table 2.2 was the most appropriate to predict the structural types. A cumulative logit model was fitted to determine the relationship between structural types (an ordinal variable) of aspen stands and predictors along the study transect. The model was implemented using the *vglm* function of the *VGAM* (Vector Generalized Additive Model) package in R version 3.1.2 (R Development Core Team, 2013). In modelling, we used a data subset of 1688 stands (observations) for which data of stand age were available in forest inventory datasets and for which we estimated the SI. These two local factors (Age and SI) appear to be determinants for

stand structural development, but they are unrelated to the group of factors (climate, fire regime and human impacts) considered at the very large geographical scale of the study area.

Model selection was conducted from a stepwise procedure. We started by identifying the predictor variable that was most significantly (lowest AIC value) related to the response variable, using univariate regression models. From the most significant variable identified, we then added other variables one by one to test if, combined or not, the constructed models could explain the distribution of structural types of aspen-dominated stands across the study transect. To avoid over-fitting, a covariate was retained only if it contributed significantly in improving the model (Burnham and Anderson, 2002). Stepwise procedure terminated when no further variable could be added. A total of 10 candidate models was retained for the final selection process, according to the order of their construction. Finally, we performed a multi-model inference in order to compare the candidate models (Mazerolle, 2006). Differences in AIC values, delta AIC (ΔAIC), and Akaike weights (W_i) among models were used to identify the model that was best supported by our dataset, using the *AICcmodavg* package of R (Mazerolle, 2011). Models with large ΔAIC values (e.g. >2) are less plausible given the data, and W_i provides an additional measure of strength of evidence for a model (Mazerolle, 2006).

Thereafter, the proportion of variance explained by each variable of interest of the best predictive model was extracted from the calculation of log-likelihoods (Burnham and Anderson, 2002), as in Equations (2.1) and (2.2):

$$\text{Variance of a variable} = 1 - R^2 \tag{2.1}$$

$$R^2 = (\text{logLik3-logLik1}) / (\text{logLik2-logLik1}) \tag{2.2}$$

where, R^2 is the (pseudo) coefficient of determination; logLik1 is the log-likelihood of the null model; logLik2 is the log-likelihood of the best model; and logLik3 is the log-likelihood of the best model, that is fitted without the variable of interest.

2.4 Results

2.4.1 Structural and compositional description of the pan-Canadian gradient

Of our 2582 studied stands, K-means has classified: 899 as having an "inverted J" structure characterizing stands dominated by stems of small DBH classes; 985 as having an "intermediate" structure characterizing stands dominated by stems of intermediate DBH classes; and 698 as having an "advanced" structure characterizing stands dominated by a wide range of diameters, often including the largest DBH (Fig. 2.2). Analysis of the distribution of structural types based on the site productivity and stand age (in Fig. 2.3) revealed that "inverted J" structure types were most frequent in younger stands (20 to 50 years old), whereas "advanced" structure types appeared more in older stands (≥ 50 years old). This interpretation led us to classify the "inverted J" types as juvenile stands and "advanced" types as mature stands. Moreover, Fig. 2.3 also shows the site productivity effect, which can shorten the forest maturation time on rich sites. It revealed that stands with a high site index (e.g., SI > 15 m) tended to reach the mature stage earlier (about 40 years), whereas those with a low site index (e.g., SI < 15 m) tended to reach the mature stage much later (about 70 years). These results suggest that on poor sites (low SI), aspen-dominated stands tend to remain within a structural stage longer before moving on to another more advanced stage, whereas the succession in the structural stages is more rapid on richer sites (high site productivity).

Fig. 2.4 shows that, contrary to our assumptions, the proportion of "inverted J" and "intermediate" structures was higher than that of "advanced" structures in the eastern

portion of the study area, including QC and ON. We observed a similar distribution pattern of structural typologies in the western (in BC) and central (in MB) portions of our study area. Conversely, regions of the Canadian boreal mixedwood that were dominated by "advanced" compared to "inverted J" aspen stands were found in AB and SK. Chi-squared tests showed that the "inverted J" structures are higher and "advanced" structures lower than expected in QC; and conversely, the "inverted J" structures are lower and "advanced" structures higher than expected in SK. The distribution pattern of structural types of aspen-dominated stands did not statistically differ in the remaining provinces relative to the expected average profile.

In terms of aspen stand composition (Fig. 2.5), no differences were observed in the proportion of "pure" aspen stands between the western (BC and AB) and eastern (QC and ON) ends of the study area. The proportion of "pure" aspen stands reached its maximum values towards the middle of the longitudinal gradient (SK and MB), whereas the proportion of "least pure" aspen stands attained its maximum values at opposing ends of this gradient (BC and QC). Further, the distribution pattern of compositional types was observed to be very similar in all studied provinces, in which "pure" aspen stands were relatively less abundant than the "least pure" aspen stands. Chi-squared test showed that the "pure" composition was lower than expected in QC; while the "pure" composition was higher and "almost pure" composition was lower than expected in MB. The distribution pattern of compositional types was not statistically different in the remaining provinces. The aspen stands with "inverted J" structures had mostly "pure" compositions (Table 2.3) and an "even-sized" distribution (Table 2.4), while those with "advanced" structures had mostly "least pure" compositions (Table 2.3) and an "uneven-sized" distribution regardless of the compositional type (Table 2.4). Particularly in SK, the "even-sized" distribution was more abundant than "uneven-sized" ones in the "advanced" structure stands of "almost pure" and "pure" compositions (Table 2.4). Only a small proportion of "advanced" stands have maintained a "pure" aspen composition, which is higher in

the middle of the transect (SK, MB) and decreases towards the eastern (ON, QC) and western (BC, AB) extremes (Table 2.4). In addition, uneven-sized pure aspen stands of advanced structure were present in all provinces.

The main companion tree species (Fig. 2.6) found in "least pure" aspen stands were paper birch (*Betula papyrifera* Marshall) and balsam fir (*Abies balsamea* [Miller] L.) in the eastern portion, and white spruce (*Picea glauca* [Moench] Voss) and balsam poplar (*Populus balsamifera* L.) in the western and middle portions of the study transect. Overall, average species richness per stand (Fig. 2.7) was roughly similar across all provinces, ranging from 2.0 to 2.6 species.

2.4.2 Prediction of stand structure and individual effect of variables

Among the candidate models considered in Table 2.5, Mod1, which combines the stand age and site productivity interaction (Age*SI), climate (DD), tree species richness (RichSp), anthropogenic disturbances (DensRoad15Km, DistRoad), and fire regime (FC), was the most significant for describing distribution of structural types in the study area. Mod1 has the highest support ($W_i = 0.53$, $\Delta AIC = 0.0$) to be the best predictive model among all candidate models. With a ΔAIC of 0.26, Mod2 is a competitor of Mod1, but has a slightly lower probability ($W_i = 0.42$) of being the best model. In fact, these two models are similar but differ in that the "FC" variable in Mod1 is replaced by the "Lat" variable in Mod2. The other candidate models had a $\Delta AIC > 2$ and a lower W_i, and they are unlikely to be the best fit for our data.

Table 2.6 displays the statistics and the effect for each variable included in the top-ranked model (Mod1, Table 2.5). All confidence intervals of these variables exclude 0, and associated *P*-values indicate that each retained predictor variable significantly improved the model ($P < 0.05$). The model-averaged estimate indicated that the stand age-site productivity interaction had a significantly positive effect on structural type. The "advanced" structure type was favored by an increase in degree-days and a decrease in road density; and is also positively associated with an increase in species

richness. Conversely, the lengthening of the fire cycle and the distance of a stand to a road negatively influenced the "advanced" structure type.

The effect of the Age*SI interaction was stronger than the individual effects of these two covariates. Apart from this local effect (expressed by Age*SI), regional climate (DD, 42.5 %), stand species richness (RichSp, 23.8 %), anthropogenic impact (DensRoad15km, 11.8 %; DistRoad, 9.5 %), and fire regime (FC, 9.1 %) also contributed significantly to the observed structural variability.

2.5 Discussion

Our results indicate that the structural distribution of aspen stands can be thought of as a product of forest dynamics and biophysical processes, with regional differences observed across the Canadian boreal mixedwood. We first discuss the local and regional factors explaining stand structure, before comparing the stand structure across Canada.

2.5.1 Local and regional factors influencing stand structure and composition

Locally, the synergy between stand age and site productivity was established as an important factor of variation in structure types of aspen-dominated stands within the Canadian mixedwood. Stand age or site productivity alone did not adequately predict the structure types in aspen stands. This finding corroborates studies conducted in other forest types which observed that structural changes do not depend solely on stand age or site productivity (Bergeron, 2000; Boucher *et al.*, 2006b). This is clearly illustrated in Table 2.1, when for example the average stand age in BC (69.2 yrs.) is higher than in AB (35.3 yrs.), however, average tree diameter is larger in AB (DBH = 18.9 cm) due to better growth conditions (SI = 23.2 m) than in BC (DBH = 16.8 cm) where tree growth is slower (SI = 17.9 m). The Fig.3 does not assume that the SI decreased with stand age, but it just shows the SI effect on the structural maturation

rates and life expectancy of the stand. Aspen-dominated stands found on productive sites would become mature and uneven-sized earlier, resulting in a more rapid emergence of shade-tolerant species within gaps, thus creating a more diverse stand than those found on less productive sites. Boucher *et al.* (2006b) argue that this is due in part to (*i*) a higher growth rate in more productive stands, which likely induces earlier senescence and thus leads to a more rapid shift to an uneven-sized structure, and (*ii*) a scarcity of resources in poor stands, which in turn reduces both the diversity of tree diameters as well as the maximum diameter that can be attained, even after the stand begins to break-up.

Besides this local effect, we also observed a strong regional effect of climate on the distribution of structural types, both directly (degree-days) and indirectly (fire cycle). The number of degree-days has an impact on tree growth duration, and by extension the structural maturation of the stand. The fact that lengthening of fire cycle is associated with the juvenile structure type (i.e. negative effect of FC) in the best predictive model (Table 2.6) seemed counter-intuitive. This does not mean that longer fire cycles are positively related to juvenile structures necessarily; but it could be due to a predominance of juvenile structures in the eastern aspen forests although this region is subjected to longer fire cycles which were supposed to promote more of mature structure types. In fact, the eastern boreal of Canada has experienced a longer history of timber harvesting (Paillé, 2012). The majority of juvenile structures in aspen forests in QC and ON would reflect forest landscapes that are largely shaped or affected by anthropogenic disturbances in this portion of the study area. This assumption is corroborated mainly by the higher road density in QC and ON compared to the other provinces (Table 2.1), suggesting an increasing pressure from human activities and their effects on forest ecosystems. The combined effects of harvesting and fire led to the simplification of forest structure (Laquerre *et al.*, 2009; Terrail, 2013) in the eastern boreal forest. Road density was also high in AB, but it would be more related to oil exploration rather than to forest exploitation (Arienti *et*

al. 2010; Latham *et al.* 2011). The distance of a stand to a road (DistRoad: another proxy for human activities) also affects forest structure; but its negative effect in Table 2.6 could be related to the sampling design of SK where aspen stands were mostly selected due to their proximity to road but show a mature structure generally. Finally, "advanced" structure type was positively associated with tree species richness; since the occurrence of companion species in tree stratum appears later in aspen stand maturation. This is due partly to inherent differences in growth rates between tree species (Varga *et al.*, 2005). In Table 2.5, the latitudinal gradient (Lat) in Mod2 also reflects a fire regime gradient, i.e. that wildfire events are more common in the northern part of the Canadian boreal forest compared to the southern part (Girardin *et al.* 2013b). This explains why FC in Mod1 is replaced by the Lat in Mod2 (Table 2.5), thus, ultimately these two models are similar.

2.5.2 Comparison between regions

As expected, juvenile aspen stands were proportionally more abundant in the western and middle portions of the study transect, due to a relatively short regional fire cycle (Table 2.1). The Chi-squared test revealed no significant differences in the structural pattern between AB and BC. Although the average fire cycles are short, many mature aspen stands found in SK were found at the ecotone between the boreal forest and the prairie grasslands, an area infrequently exposed to fire (fire cycle > 1000 yrs., Table 2.1).

Conversely, the observed low proportion of mature aspen stands in QC and ON cannot be explained by the regional fire regime (Table 2.1). It is likely the result of a long history of human colonization and forest management practices in the region (Paillé, 2012) that has resulted in a reduction of a large part of the old, often structurally complex natural forest across the landscape (Bose *et al.*, 2014; Gauthier *et al.*, 2009). Human activities have contributed to the transformation of eastern forest landscapes since the early twentieth century, by rejuvenating and altering the forest

composition in the affected areas (Boucher *et al.*, 2006a; Laquerre *et al.*, 2009; Terrail, 2013). Forest management and human colonization may thus explain the low impact of the existing fire regime in the eastern boreal forest, by creating a distribution pattern more typical of one found under a shorter fire cycle, dominated by younger stands rather than old forests.

Cumming *et al.* (2009) report that the canopies of upland mesic sites in the boreal mixedwood forests of western Canada are dominated by some combination of *Populus* species (typically trembling aspen, but at times balsam poplar) and white spruce. Like these authors, we also found that white spruce and balsam poplar are the main companion tree species associated with the least pure aspen stands category in western Canada (Figure 2.6). Balsam fir and paper birch (mainly on coarse deposits) were their equivalent in east (Bergeron *et al.* 2014).

High proportions of pure aspen stands observed in SK and MB (Figure 2.5, Table 2.4) is the result of low conifer recruitment in this region (Nlungu-Kweta et al. 2014). This is probably due to severe drought conditions that reduce the growth and survival of conifer seedlings, and intense competition from bluejoint grass (*Calamagrostis canadensis* [Michx.] P.Beauv.).

Overall, a small proportion of observed mature, old aspen forests have evolved into a multi-layered (uneven-sized) structure without compositional change. This phenomenon of multi-cohort pure aspen forests was observed throughout the entire Canadian boreal mixedwood forest (Table 2.4), supporting observations made by Cumming *et al.* (2000) in British Columbia, and LeBlanc (2014) in Manitoba. The theory of gap dynamics is highlighted, by suggesting a mechanism whereby old, uneven-aged aspen stands could develop and persist, in the absence of shade-tolerant and other hardwood competitors (Moulinier *et al.* 2011). Most aspen regeneration is clonal, via root suckers that can be subsidised by canopy trees (Frey *et al.*, 2004; Peterson and Peterson, 1992). Therefore when even a small gap is created in the

canopy, and there is an absence of competitors, aspen will fill the openings by root suckering to form a new cohort, generating an uneven-sized and spatially heterogeneous age structure.

2.6 Conclusion

This study revealed that the distribution pattern of aspen-dominated stand characteristics was similar between western and eastern portions of the Canada's boreal mixedwood, despite a marked contrast in climatic conditions and fire regime.

The effects of regional climate and associated disturbance regimes affect variously the forest ecosystem under study along an east-west transect. The western aspen forests remained mainly shaped by frequent wildfires, while the distribution of stand structural types of eastern aspen forests does not correspond with the dominant fire regime (long FC) in this region. The finding in eastern Canada suggests that human activities can decouple the link between natural disturbance regime and the ecosystem, by superimposing a new disturbance regime upon the pre-existing natural one. The potential effects of altered fire regime due to climate change on forest characteristics could be more significant in the eastern aspen forests, where the cumulative effects of fire and forest harvesting have already simplified stand structure to similar proportions as fire alone does in the western aspen forests. Besides the effects of fire regime and human activities, the site's richness appeared as a significant factor affecting the forest structural maturation rate.

2.7 Acknowledgements

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Figure 2.1 Map of the study area, along an east-west transect in Canada. The "boreal mixedwood" (dark grey area) corresponds to the thermoboreal bioclimatic subdivision of the Canadian boreal biome (Baldwin et al., 2012). Black dots represent our study sites.

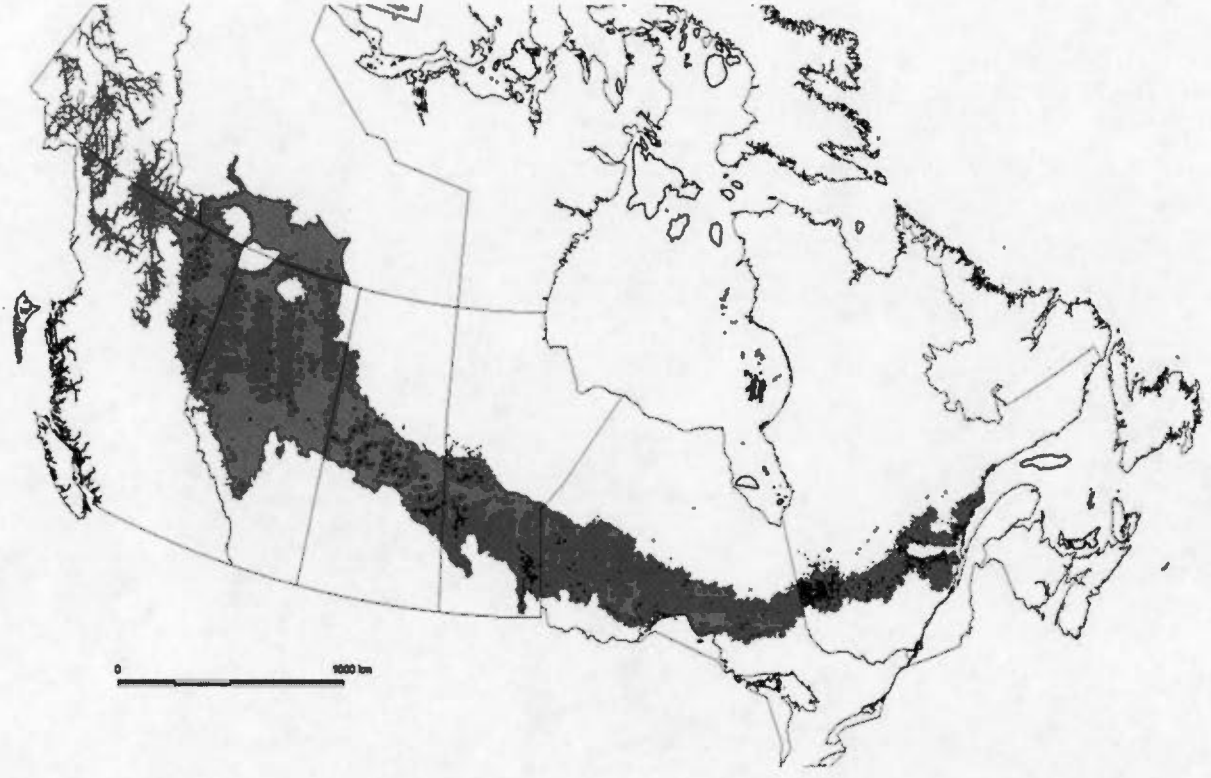

Figure 2.2 Mean diameter distributions corresponding to the three types of stand structure. Black bars represent the "inverted J" structure, gray bars represent the "intermediate" structure and hatched bars indicate the "advanced" structure.

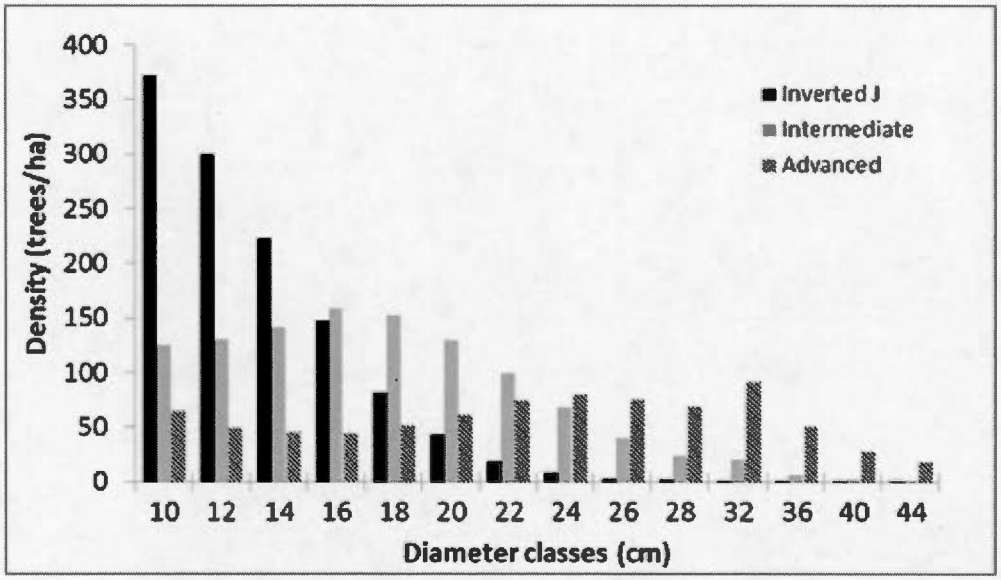

Figure 2.3 Distribution of structural types based on the site productivity and stand age. 1688 aspen stands were used in analysis; including 603 "inverted J" (diamond), 650 "intermediate" (square) and 435 "advanced" (triangle) structure.

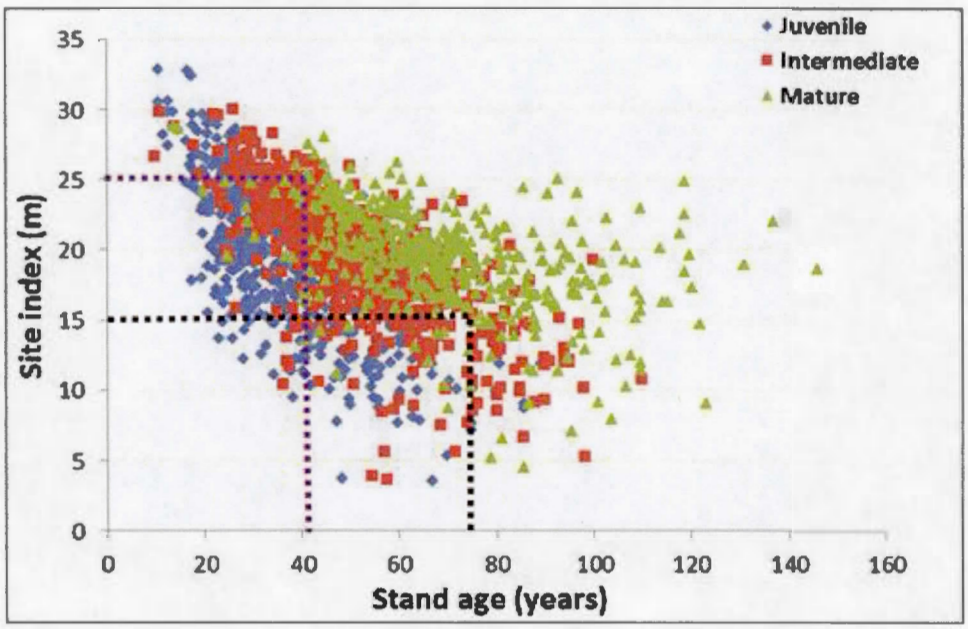

Figure 2.4 Relative frequencies of structural types by province throughout the longitudinal gradient. Black bars represent aspen stands with "inverted J" structure; gray bars represent aspen stands with "intermediate" structure and hatched bars indicate aspen stands with "advanced" structure. The stars above bars refer to statistic Z (Freeman-Tukey deviates). They identify structural types of provinces (Quebec and Saskatchewan) in which the number of observations significantly ($p < 0.05$) differs (higher or lower) from the corresponding expected frequency.

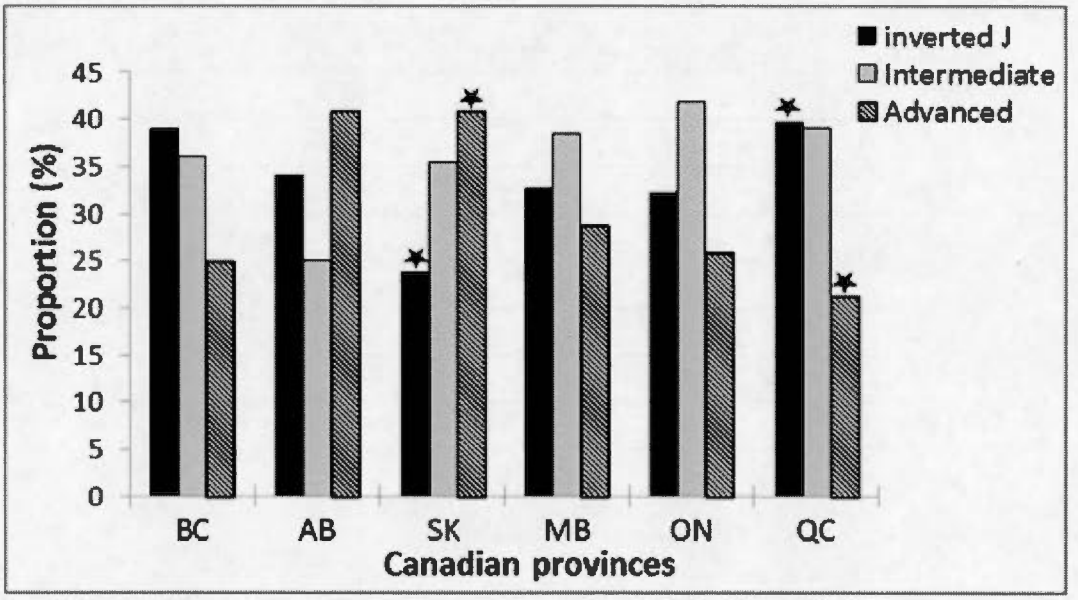

Figure 2.5 Relative frequencies of compositional types by province throughout the longitudinal gradient. Black bars represent "least pure" aspen stands; gray bars represent "almost pure" aspen stands and hatched bars indicative "pure" aspen stands. The stars above bars refer to statistic Z (Freeman-Tukey deviates). They identify compositional types of provinces (Quebec and Manitoba) in which the number of observations significantly ($p < 0.05$) differs (higher or lower) from the corresponding expected frequency.

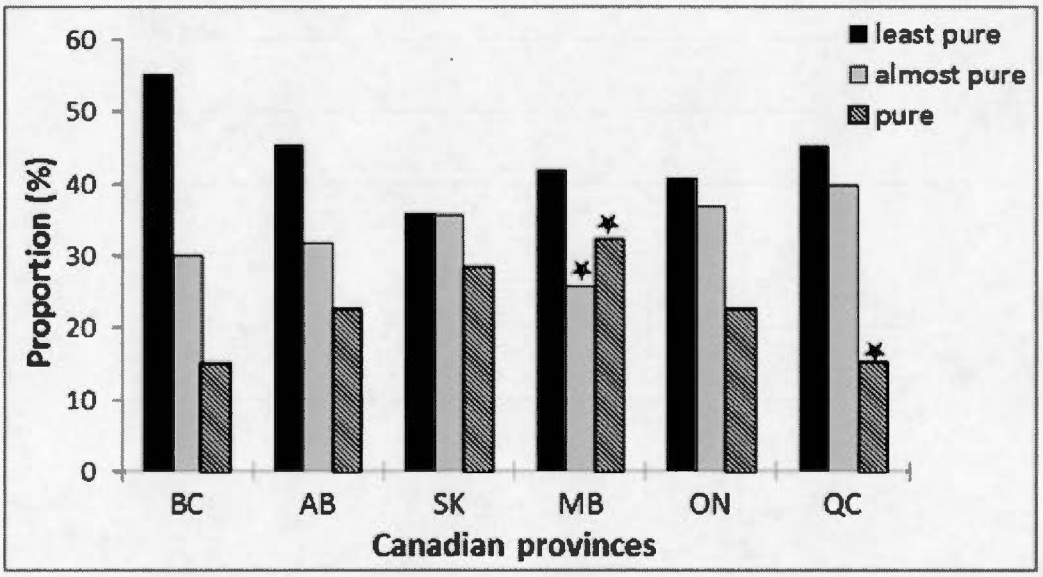

Figure 2.6 Proportion (%) of "least pure" aspen stands with the main companion tree species. The "WB" refers to aspen-dominated stands where paper birch (Betula papyrifera) is main companion tree species; and so on for "BA" as balsam poplar (Populus balsamifera), "BF" as balsam fir (Abies balsamea), "WS" as white spruce (Picea glauca), "BS" as black spruce (Picea mariana), and "JP" as jack pine (Pinus banksiana).

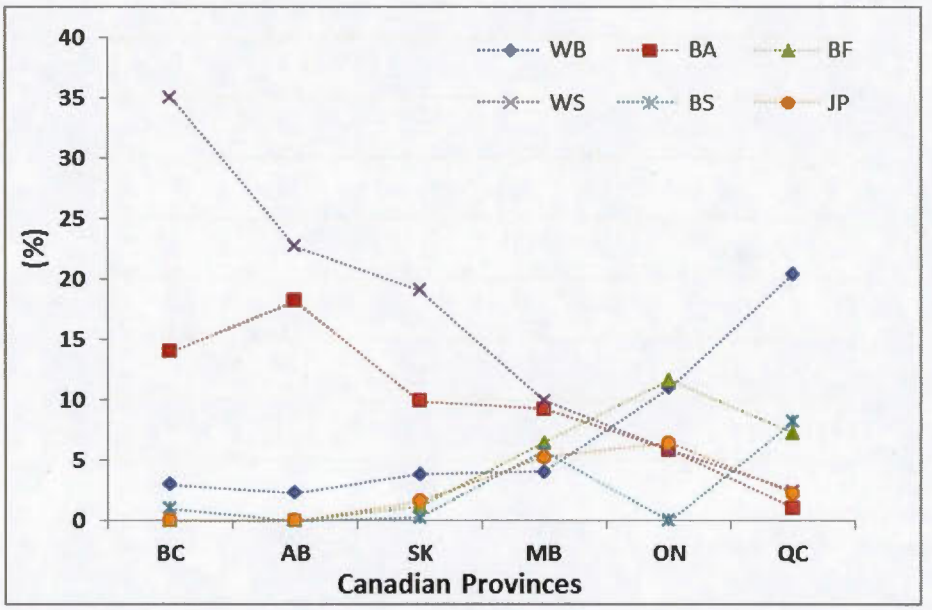

Figure 2.7 Variability in average species richness per stand in a province. The black diamonds designate the number of tree species, while the black line on each diamond represents two standard deviations to indicate the degree of variability existing in stands within a province.

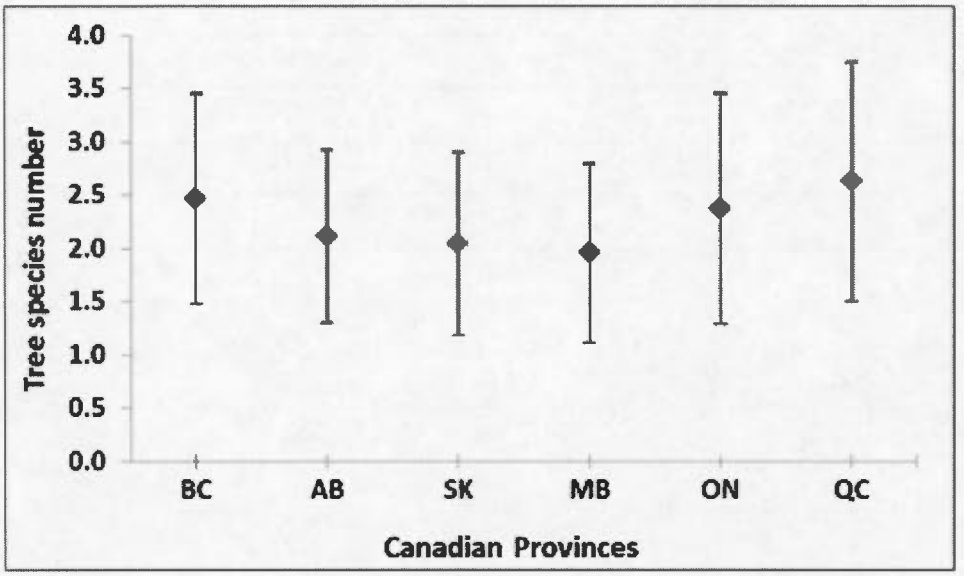

Table 2.1 Stand and environmental characteristics [mean and (range)] of examined stands by Canadian province.

Provinces[a]	No. of stands[b]	DBH (cm)	Age (years)	Site index (m)[c]	Degree-Day (°C day)[d]	Fire cycle (years)	DistRoad (Km)[e]	DensRoad15Km (Km)[f]	DensRoad25Km (Km)[g]
BC	100	16.8 (9-60.1)	69.2 (21 - 146)	17.9 (11.2-25.0)	2117.2 (1771.7-2296.8)	387.4 (326.8-397.9)	5.3 (0-45.1)	81.0 (5.7-513.9)	209.4 (13.6-1151.6)
AB	44	18.9 (9-56.2)	35.3 (25 - 124)	23.2 (11.4-32.8)	2237.3 (2041.9-2375.9)	332.7 (93-672.9)	1.7 (0-13.9)	158.3 (6.6-410.3)	448.3 (68.5-1114.3)
SK	446	17.3 (9-81.2)	59.9 (19 - 102.1)	16 (7.5-25.3)	2290.8 (2140.9-2425.8)	301.9 (50.9-1225.6)	1.1 (0-9.6)	127.6 (1-427.8)	336.1 (7.5-1402.4)
MB	574	16.6 (9-63.9)	56.1 (19.7 - 123.3)	16.7 (7.1-26.7)	2477.5 (2057.8-2801.1)	325.7 (56.2-1225.6)	3.8 (0-29.6)	119.2 (2.4-479.1)	334.6 (9.7-928.7)
ON	155	16.5 (9-56.7)	50.9 (32.4 - 133)	19.2 (17.2-22.6)	2401.8 (2133.6-2663.2)	748.3 (83.9-1440.2)	3.1 (0-29.1)	169.4 (19.9-447.5)	467.2 (38.1-1100.8)
QC	1263	18.1 (9-84.1)	43.5 (16.6 - 162)	22 (12.5-32.8)	2296 (1884.5-2562.9)	1360.5 (625.7-3706.6)	1.8 (0-74.7)	289.3 (0.5-1199.3)	762.5 (6-2654.5)
Total or ranges	2582	9-84.1	16.6 - 162	7.5-32.8	1771.7-2801.1	50.9-3706.6	0-74.7	0.5-1199.3	6-2654.5

[a] BC (British Columbia), AB (Alberta), SK (Saskatchewan), MB (Manitoba), ON (Ontario) and QC (Quebec). [b] Number of study aspen stands (observations) per province. In these observations, only 91in BC, 40 in AB, 214 in SK, 452 in MB, 91 in ON, and 800 in QC for which the stand age (Age) was available (i.e. only 1688 over 2582 stands in total). [c] is a measure indicating the site productivity; defined as mean height of trees at reference age of 50-years. [d] is the cumulative degree-days above 5°C.[e] is the distance from the stand relative to the nearest main road. [f] and [g] denote road density in a radius of 15 and 25 km around the stand, respectively. For the inventory data used in the study, the range of the survey years varies from one province to another; i.e. between 1980-2009 in QC, 1992-2006 in ON, 2002-2011 in MB, 1978-2000 in SK, 2001-2008 in AB, and 1970-2008 in BC.

Table 2.2 Types and description of predictor variables used in modeling structural types.

Variable (abbreviation)	Description	Data source
	Climatic	
Aridity index (AI)	Annual mean aridity (1981-2010) (mm)	Environment Canada 2013
Degree-days (DD)	Annual mean degree-day over 5°C (1981-2010) (°C day)	Environment Canada 2013
	Fire regime	
Fire Cycle (FC)	Year interval from cyclic return fire (Years)	Boulanger *et al.* 2012
	Physical environment	
Distance to the nearest great river, lake or bay (DistWater)++	Distance to the nearest significant watercourse (Km)	Natural resources of Canada - Geobase
Hydrography (PctHydro)	Percentage of area occuped by water in a radius of 15 Km around the stand (%)	Natural resources of Canada - Geobase
	Anthropogenic	
Distance to the nearest main road (DistRoad)	Distance to the nearest carriage road (Km)	Natural resources of Canada - Geobase
Distance to agricultural area (DistAgri)	Distance to the nearest farmland (Km)	Natural resources of Canada - Geobase
Road density (DensRoad)	Total length of roads (Km) / Km^2 area, in a radius of 15 and 25 Km around the stand	Natural resources of Canada - Geobase
	Spatial	
Longitude (Long)	Geographic coordinates	Forest inventory datasets
Latitude (Lat)	Geographic coordinates	Forest inventory datasets
Elevation (Elev)	Geographic coordinates	Forest inventory datasets
	Others	

Tree species richness (RichSp)	Number of trees species found within the stand	Tree species number counted in the stand
Stand age (Age)	Time since the last major disturbance (years)	Forest inventory datasets
Site index (SI)	Mean height of aspen stem at 50 years (m)	Estimated as in Nigh *et al.* (2002)
(Age*SI)	Interaction between stand age and site productivity	Age multiplied by SI.

[++]The size of the watercourse considered in the analysis ranged from 5 to 35,000 Km^2 (an average of about 340 Km^2). Data on anthropogenic variables and those describing the physical environment were mainly sourced from the GeoBase of Natural Resources Canada. http://www.geogratis.ca/goegratis/DownloadDirectory?lang=fr.

Table 2.3 Frequency (%) of aspen stands (n=2582) composition according to structure types.

		Structure		
		Inverted J	Intermediate	Advanced
Composition	Pure	**29.6**	19.4	15.4
	Almost pure	37.8	37	29.4
	Least pure	32.6	43.6	**55.2**

Values in boldface indicate compositional class in which there is the highest proportion of aspen stands for "Inverted J" and "Advanced" structural types, respectively.

Table 2.4 Numbers and frequencies (%) of even- and uneven-sized stands by structure type.

Prov.	"Inverted J" structure			"Advanced" structure									
					By compositional type (%)			*Within compositional type (%)*					
								Least pure		Almost pure		Pure	
	Nb. of stands	Even-sized (%)	Uneven-sized (%)	Nb. of stands	Least pure	Almost pure	Pure	Even-sized	Uneven-sized	Even-sized	Uneven-sized	Even-sized	Uneven-sized
BC	39	89.7	10.3	25	72.0	24.0	4.0	4.0	68.0	8.0	16.0	0.0	4.0
AB	15	93.3	6.7	18	61.1	27.8	11.1	22.2	38.9	5.6	22.2	5.6	5.5
SK	106	99.1	0.9	182	42.3	34.6	23.1	9.9	32.4	19.8	14.8	18.2	4.9
MB	188	90.4	9.6	165	47.9	28.5	23.6	5.5	42.4	1.8	26.7	1.2	22.4
ON	50	96.0	4.0	40	52.5	35.0	12.5	20.0	32.5	7.5	27.5	2.5	10.0
QC	501	80.4	19.6	268	66.0	27.6	6.3	6.7	59.3	2.2	25.4	0.7	5.6
Total	899			698									

Frequency is the ratio of the number of even- or uneven-sized stands over the total number of stands in each structural type by province. Critical Value of the Pearson Product-Moment Correlation Coefficient at df= n-2 was 0.553 (at $p < 0.05$ and n=13 i.e. 14 DBH classes minus 1).

Table 2.5 List of models and results of model selection based on AIC criteria to explain the pattern of structural types distribution. K: number of estimated parameters included in the model; LL: log-likelihood value of the model; AIC: Akaike's information criterion value; ΔAIC: delta AIC, a measure of the model relative to the best model; Wi: AIC model weight, representing the ratio of the ΔAIC of the model relative to the whole set of candidate models.

Candidate Models	Model ID	K	LL	AIC	ΔAIC	W_i
Age*SI+DD+RichSp+DensRoad15Km+DistRoad+FC	**Mod1**	**8**	**-1256.54**	**2529.16**	**0.00**	**0.53**
Age*SI+DD+RichSp+DensRoad15Km+DistRoad+Lat	Mod2	8	-1256.67	2529.42	0.26	0.42
Age*SI+DD+RichSp+Long	Mod3	6	-1260.53	2533.12	3.96	0.07
Age*SI+DD+RichSp+DensRoad15Km+FC	Mod4	7	-1260.25	2534.58	5.41	0.03
Age*SI+DD+RichSp+DensRoad15Km	Mod5	6	-1262.53	2537.11	7.95	0.01
Age*SI+DD+RichSp+FC	Mod6	6	-1264.03	2540.12	10.95	0.00
Age*SI+DD+RichSp	Mod7	5	-1268.38	2546.79	17.63	0.00
Age*SI+DD+AI	Mod8	5	-1269.00	2548.04	18.88	0.00
Age*SI+DD+FC	Mod9	5	-1272.43	2554.90	25.73	0.00
Age*SI	Mod10	3	-1295.56	2597.14	67.98	0.00

Models are ranked based on their AIC scores, where the smallest AIC represents the best model (in bold).

Table 2.6 Model-averaged estimates of the explanatory variables of the parsimonious model (Mod1) and their 95% confidence intervals (CI), as well as their variance partitioning.

Covariates	Estimate	Lower 95% CI	Upper 95% CI	*P* value	Variance (%)
Age*SI	0.0065	0.0060	0.00703	< 0.000	N/A
DD	0.0021	0.0014	0.00283	< 0.000	42.5
RichSp	0.2226	0.1205	0.32471	< 0.000	23.8
DensRoad15Km	-0.0012	-0.0019	-0.00040	0.003	11.8
DistRoad	-0.0386	-0.0670	-0.01024	0.008	9.5
FC	-0.0001	-0.0002	-0.00003	0.009	9.1

All variables are significant at $P < 0.05$, based on the z test. Variance is the proportion of variability explained by variable in the model, as defined in Eq. (1) and (2). In the estimation of variances, the interaction Age*SI was considered as the parameter of the null model because Age and SI are co-factors unrelated to our study assumptions, and which we want to control the effect. N/A: not applicable.

APPENDICE B.1.

Distribution of aspen stands [mixed and aspen-dominated stands, respectively having ≥ 50 % and ≥ 75 % of total basal area in aspen] per province, based on the study area and data selection.

Provinces	Type of aspen stands		Total [(1)+(2)]	Std dev. of mixed stands in aspen	% least pure aspen stands following table 2.4
	mixed (1)	aspen-dominated (2)			
BC	326	100	426	0.77	0.71
AB	63	44	107	0.59	0.61
SK	745	446	1191	0.63	0.42
MB	1008	574	1582	0.64	0.48
ON	228	155	383	0.6	0.52
QC	4424	1263	5687	0.78	0.66
Total	6794	2582			

We also calculated the correlation between data used in the thesis [i.e. (2)] and those obtained following the addition of between (1) and (2). This correlation in terms of the mixed composition is **0.6998**, which is nevertheless reassuring for the portrait of Canadian aspen stands from data used in the thesis.

CHAPITRE III

IMPACT OF CLIMATE AND SOIL PROPERTIES ON ASPEN (*Populus tremuloides* Michx.) HEIGHT GROWTH ALONG AN EAST-WEST TRANSECT IN CANADA'S FOREST.

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3.1 Abstract

Boreal ecosystems are particularly sensitive to climate variations. Projected climate change in boreal regions, in particular, changes in the precipitation regime, is expected to affect tree growth. This study sought to evaluate the variability in aspen (*Populus tremuloides* Michx.) height growth in response to climate and soil physical and chemical properties along a longitudinal gradient across Canada's forest. In each stand, aspen height growth was expressed as site index, which was derived from stem analysis data. We found that the factors limiting aspen height growth varied at different spatial scales, as a function of the interaction between climate and local soil conditions. Overall, aspen height growth was higher in the eastern and western ends of the longitudinal gradient than in central Canada. Mean annual precipitation was identified as a major factor influencing aspen height growth, although the soil phosphorus availability also appeared to be a factor constraining this growth. Some environmental factors such as the mean temperature and soil texture were not significant on aspen height growth in part due to their weak variations among our sites and aspen's ability to improve site productivity.

Key words: aspen height growth, boreal forest, climate, forest productivity, soil properties.

Résumé

Les écosystèmes boréaux sont particulièrement sensibles aux variations climatiques. Les changements climatiques prévus dans les régions boréales, en particulier, des changements dans le régime des précipitations, devraient affecter la croissance des arbres. La présente étude visait à évaluer la variabilité dans la croissance en hauteur du tremble (*Populus tremuloides* Michx.) en réponse au climat et aux propriétés physiques et chimiques du sol, le long d'un gradient longitudinal à travers la forêt du

Canada. Dans chaque peuplement, la croissance en hauteur du tremble était exprimée par l'index de qualité du site, dérivé à partir des données de l'analyse de tige. Nous avons trouvé que les facteurs limitant la croissance en hauteur du tremble varient à différentes échelles spatiales, en fonction de l'interaction entre le climat et les conditions locales du sol. Globalement, la croissance en hauteur du tremble était plus élevée dans les extrémités est et ouest du gradient longitudinal que dans la partie centrale du Canada. Les précipitations annuelles moyennes ont été identifiées comme un facteur important influençant la croissance en hauteur tremble, bien que la disponibilité du phosphore du sol semble également être un facteur contraignant cette croissance. Certains facteurs environnementaux tels que la température moyenne et la texture du sol n'étaient pas significatifs sur la croissance en hauteur du tremble, en partie en raison de leurs faibles variations entre nos sites d'étude et à la capacité du tremble à améliorer la productivité du site.

Mots-clef: croissance en hauteur du tremble, forêt boréale, climat, productivité forestière, propriétés du sol.

3.2 Introduction

In North America, forest ecosystems are tightly coupled with climate both directly through the effects of temperature and precipitation and indirectly through the effects of disturbances (Gauthier *et al.* 2014). Trembling aspen or aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America (Perala 1990). It is especially abundant in the Canadian boreal forest, where its ecological and economic importance has increased in the last decades (Peterson and Peterson 1992). Ongoing climate change with regional shifts in temperature and precipitation both in direction and magnitude (Gauthier *et al.* 2014) affects growth of this key tree species of the boreal forest. Projected changes in climate for the coming decades are greater than those experienced over the last 100 years (Price *et al.* 2011; IPCC 2013), and therefore, are expected to have significant impacts on the tree growth and forest dynamics in the Canadian forests (Papadopol 2000; Gauthier *et al.* 2014). These impacts may vary according to the forest species composition and spatial environment (Messaoud and Chen 2011). Studies carried out in the prairie provinces of Canada (Alberta, Saskatchewan, and Manitoba) showed that drought and/or long-term decreasing climate moisture availability was one of the major factors causing reduced growth of trembling aspen (Hogg *et al.* 2008; Hogg *et al.* 2013; Worrall *et al.* 2013, Chen and Luo 2015), whereas warming was identified as the major driver of aspen growth in aspen-dominated stands in eastern Canada (Lapointe-Garant *et al.* 2010). Besides climate, local site conditions such as soil properties play a major role in tree growth (Paré *et al.* 2001; Pinno *et al.* 2009; Pinno and Bélanger 2011), as well as in forest maturation rate. Chen *et al.* (1998a) found that aspen site index increased with increasing soil nutrient availability on slightly dry sites and with increasing available soil moisture on poor sites.

Previous studies on aspen height growth-environmental factors relationship in Canada's boreal were conducted in relatively limited regions, often at local landscape (e.g., Chen *et al.* 1998a; Paré *et al.* 2001; Pinno *et al.* 2009; Pinno and Bélanger 2011;

Anyomi *et al.* 2012) and provincial (e.g., Chen *et al.* 2002; Hogg *et al.* 2008; Hogg *et al.* 2013) spatial scales. Analysing forest growth along a wide gradient of environmental conditions gives a better understanding of the way in which boreal ecosystems are responding to ongoing global changes. This study covers a very wide longitudinal gradient at the pan-Canadian forest scale. Longitudinally, the most important change in climate across the North American boreal forest is the change in precipitation regime, more than in temperature (Hart and Chen 2006). There is a strong precipitation gradient, from a drier west to moister conditions in the east of Canada (Environment Canada 2013). The eastern part of Canada is characterized by a humid climate (Bergeron and Flannigan 1995); whereas the western part is subject to warmer and drier air masses (Chhin et al. 2008). Since moisture balance was reported to be a significant factor controlling aspen growth (Hogg and Bernier 2005), we therefore hypothesized that aspen height growth would be better in eastern part of the longitudinal transect compared to the interior and western Canada. Further, since aspen can be found on a wide variety of soil types (Pinno et al. 2009), we also hypothesized that aspen height growth would vary among and within regions along the longitudinal gradient of Canada, based on soil's nutritional attributes.

The objectives of this study were to (i) determine aspen height growth patterns along an east-west transect through the Canadian forest, with wide variability in climatic conditions and soil properties; (ii) identify among the selected environmental measurements, the major factors driving the variation in aspen height growth along the study longitudinal transect.

3.3 Materials and Methods

3.3.1 Study area and stands selection

The studied stands were deliberately selected at various locations throughout the pan-Canadian gradient to capture the widest range of precipitation possibly found along the longitudinal transect in Canada's forest. To develop a stratified sampling strategy, we used BIOSIM 9 (Régnière and Saint-Amant 2008) to generate mean of annual total precipitation (MAP) using the database "Normals" from 1981 to 2010 (10,000 points; 5 replicates) of Environment Canada to produce a map with polygons of MAP grouped into classes of 50-mm intervals (e.g. 400, 450, 500, and so on). In ArcGIS, eco-forest maps, MAP polygons of precipitation classes, and other available information were superimposed for selecting the study sites. A total of 49 aspen stands, including six in the aspen parkland, were selected along the continuous boreal forest extending from Québec's North-shore in the eastern to the northeastern British Columbia in western Canada (Fig. 3.1). In each Canadian province of study, a minimum of one stand was selected per precipitation class with the following criteria: stands naturally established with ease of access, at least 1 ha in area, unmanaged, dominated by aspen (≥ 75 % basal area in aspen), mature (at least 50 yrs-old) without a history of suppression or damage, and on mesic soil.

Climatic factors vary among and within the Canadian provinces (Environment Canada 2013). Precipitation increases towards the eastern portion, whereas in the central and western portions, the limiting climatic factor is moisture availability more than temperature. For this study, stand characteristics were grouped according to province for illustrating the longitudinal transect (Table 3.1). Mean annual total precipitation (MAP) was higher in eastern (QC and ON) compared to central (MB and SK) and western Canada (AB and BC); and conversely, annual water deficit (WD) which is the accumulated monthly water deficit (i.e. monthly Thornthwaite potential evapotranspiration minus monthly precipitation) was highest in western and central provinces compared to eastern provinces; while mean annual temperature (MAT) was relatively similar for all provinces (from about 1 ± 0.8 °C).

3.3.2 Field sampling and laboratory analyses

A circular (radius = 11.28 m) sampling plot was randomly established in each sample stand, located at least 50 m away from road and other openings to avoid edge effects. Within the plot, all live trees with a diameter at breast height (DBH) ≥ 9 cm were counted and their DBH were measured for stand density and basal area calculations. Three dominant aspen trees located adjacent to but outside of plot were felled for stem analysis. These dominant trees were defined as having no visible growth abnormalities or damage, but not necessarily the biggest to avoid sampling of survivors (veterans) or genetically superior trees. The sample trees were cut at the ground level, total tree heights were measured in after felling. And stem disks (cross-sections) were taken at stump height (stand age determination) and 1.3 m and at every meter thereafter until the diameter outside the bark was less than 2 cm.

Within each sample plot, four samples of the mineral soil (0-30 cm, beneath the organic matter) were taken at various locations within the plot and pooled to form one sample per sampling plot for soil texture and nutrients analyses. This soil depth was chosen because sampling was possible to this depth at all sites and because this portion of the soil contains many fine roots.

Soil property analyses were conducted in the laboratory. Mineral soil samples were air-dried and sieved with a 2-mm mesh to remove any coarse fragments (e.g. twigs, needles, gravel). They were analyzed for soil texture (sand, silt and clay contents) and pH in water. Total carbon (C) and nitrogen (N) was determined by dry combustion and infrared detection using the Leco CNS-2000 (1100 °C). The exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+}) were analyzed using atomic absorption/emission, and extractable phosphorus BRAY II was analyzed colourimetrically (molybdenum blue).

3.3.3 Determination of site index

In each stand, aspen height growth was expressed by its site index (SI), which is tree height at 50 years from the root collar and derived from stem analysis data in the laboratory. SI is considered the best indicator for potential productivity of forest stands, since it is not dependent on the stocking (McKenney and Pedlar 2003; Skovsgaard and Vanclay 2008). In the laboratory, each stem disc was sanded with successively finer grades of sandpaper to expose two, clear radial sections, from pith to bark. The number of growth rings was counted in the two directions for each disk with a binocular microscope. From there, raw stem analysis data were adjusted using Carmean's (1972) algorithm to calculate tree height corresponding to the age at each sectioned disk. The height versus age curves for the three sampled trees per stand were carefully examined for uniformity and the presence of suppression or damage. A linear interpolation method was used to develop an average curve for each sample plot using Carmean's correction. Stand-level aspen site index was determined from the mean of height of trees at 50 years. Since aspen is a fast growing pioneer species and regenerate at the same time following fire, we considered the highest age of stem disc at stump height among the 3 trees felled as being stand age.

3.3.4 Explanatory variables

The variability in aspen height growth (response variable) throughout the longitudinal gradient in Canada was investigated depending on environmental factors (independent variables) such as climate, mineral soil properties, as well as spatial gradients. The mean values of these factors per Canadian province are shown in Table 3.1. For each study stand, climate data (mean annual for a period of 30 years, 1981-2010) were generated using BioSIM 9 from Environment Canada data (Environment Canada 2013) - and include mean annual total precipitation (MAP), mean annual temperature (MAT), relative humidity (H°), growing degree-days at 5°C (GDD), and water deficit (WD). Mineral soil properties include measures of soil texture (sand, silt and clay contents), nutrients [carbon-nitrogen ratio (C:N), Bray II extractable phosphorus (P), cation exchange capacity or the sum of exchangeable

cations (CEC), and pH water], as indicated previously. The longitude, latitude and elevation have been added as climatic surrogates to observe whether the response variable also varied with respect to the indirect effect of spatial scale.

3.3.5 Data analysis and model selection

Simple regression was performed to examine the suite of environmental factors most closely related to aspen height growth for all 49 studied stands and Pearson's correlation analysis was used to examine the degree of correlation between environmental factors. Then multiple regression models were developed to identify the major environmental factors influencing aspen height growth throughout the pan-Canadian gradient, based on Akaike's Information Criterion (AIC).

For model selection, we first implemented univariate regression models for verifying which variable was the most significantly (lowest AIC value) related to the response variable. From the most significant variable(s) identified, we then added other variables one by one to test if, combined or not, the constructed models could explain the variability in aspen SI along the study longitudinal transect. To avoid over-fitting, a covariate was retained only if it contributed significantly (AIC decreased by at least 2) in improving the model (Burnham and Anderson, 2002). Stepwise procedure terminated when no further variable could be added. Ten candidate models were retained for the final selection process, according to the order of their construction. Finally, we performed a multi-model inference in order to compare the candidate models (Mazerolle, 2006). Differences in AIC values, delta AIC (ΔAIC) and Akaike weights (W_i) of candidate models were used to identify the predictive model that best fits our dataset, using the *AICcmodavg* R package (Mazerolle, 2011). We also estimated the explained variance proportion by each explanatory variable of the best model. All statistical analyses were implemented using R version 3.1.3 (R-Development-Core-Team 2014).

3.4 Results

3.4.1 Stand characteristics and variability in aspen height growth

In Table 3.1, stand characteristics indicate that aspen average- and total -basal areas were higher in eastern sites (39.1, 45.1 for stands located in QC and 38.8, 43.6 for those in ON, respectively), compared to the central (27.4, 28.7 for stands located in MB and 23.0, 24.1 for those in SK, respectively) and western (25.9, 27.7 for stands located in AB and 16.2, 16.3 for those in BC, respectively) sites of the study area. In contrast, stand density varied from one region to the next without an apparent longitudinal trend across the gradient of Canada.

We found that the aspen SI estimated for each stand had varied considerably throughout the study area and ranges from a minimum of 11.9 m, located in aspen parkland, to a maximum of 26.5 m. However, mean aspen SI (shown in Table 3.1) was low among stands located in central portion (MB and SK) as compared to ones in eastern (QC and ON) and western (BC and AB) extremities of the longitudinal gradient of the study area. The mean aspen SI in studied stands of BC and AB is comparable to that of QC and ON, and reaches its maximum values at opposing ends of the gradient (BC and QC). It further appeared that aspen SI were generally lowest in stands located in aspen parkland versus those in the continuous boreal, even within Canada's Prairie Provinces (MB, SK and BC).

3.4.2 Relationship between aspen height growth and environmental factors

Simple regression analysis for all studied stands indicated that latitude among the spatial variables and available phosphorus among the soil properties, had a weak significant effect ($P < 0.1$) on the aspen SI; whereas effects of annual total precipitation ($P < 0.01$) and relative humidity ($P < 0.05$) among climate variables were most significant. The combination of variables of climate, soil and spatial gradient has strengthened this effect of annual total precipitation ($P < 0.001$) and available P ($P < 0.05$). Correlation analysis (Table 3.2) showed that aspen height

growth (aspen SI) was significantly and positively related to the annual total precipitation (r = 0.38) and available phosphorus (r = 0.37), and negatively to the water deficit (r = -0.38) among measured environmental factors. There was no significant correlation (main effect) between aspen height growth and the spatial variables, mean temperature, relative humidity, growing degree-days, carbon:nitrogen ratio, soil pH, cation exchange capacity, and soil texture within our study dataset. Note that the annual precipitation was very strongly and negatively correlated with water deficit (r = -0.91) and positively correlated with relative humidity (r = 0.73). The water deficit, which is accumulated monthly water deficit, was inversely related to the relative humidity (r = -0.63) among our study sites.

3.4.3 Predicting aspen height growth for the pan-Canadian stands

The multi-model inference analysis (Table 3.3) showed that Mod1 combining annual total precipitation (MAP), latitude (Lat) and concentration of mineral soil's available phosphorus (P) has the highest substantial evidence (ΔAICc: 0.0) to be the most parsimonious model for describing the variability in aspen height growth along the east-west transect of Canada. The Mod1 has a 54% (W_i: 0.54) chance of being the best one among those considered in the set of candidate models. It accounts for 40 % (R^2 adjusted: 0.4) of the observed variability in aspen height growth. The second best model (Mod2) according to its ΔAICc (2.03) score garnered only a 20 % (W_i: 0.2) chance of being the best one. However, with a ΔAICc > 2, the other remaining candidate models were unlikely to be the best predictive model. The WD (Mod9) or MAP (Mod10) alone was not enough to predict aspen height growth, and none of the soil texture variables (soil properties) was retained within candidate models to predict aspen height growth in this study. Further, a statistical collinearity was observed between mean annual precipitation and water deficit variables.

In Table 3.4, the model-averaged estimate indicates that aspen height growth increased positively with the MAP, lat. and available soil P. The *t*-test showed that

these parameters have significantly helped to improve the model fitting ($P < 0.05$) and that there was a strong effect of each explanatory variable on response variable. The confidence intervals have excluded 0, corroborating that the response variable (aspen SI) varied with these three explanatory variables identified above. Climatic conditions (MAP: 74.1 % and Lat: 40.5 %) explained most of the observed variability in the aspen height growth compared to the soil nutrient (available P: 33.3 %).

3.5 Discussion

In natural ecosystems, the multiple dimensions of environmental variables and interactions among the variables, their temporal and spatial variability, and vegetation feedback often impose uncertainty in examining cause–effect relationships between tree productivity and environmental variables (Chen *et al.* 1998a; Anyomi *et al.* 2014). We discussed the relationships between aspen height growth and environmental factors across the pan-Canadian scale in the manner below.

The variability observed in aspen height growth would result from the variety of local site conditions and the potential clonal diversity among aspen stands (Latutrie *et al.* 2015) as found across the forests in Canada, given the wide scale of study area. However, the low mean aspen height growth observed in stands of the central boreal forest (MB and SK) may be attributable mainly to the water deficit (higher water deficit), following the low amount of annual precipitation in this region of Canada (see Table 3.1). Hogg *et al.* (2008) also observed a 30% decrease in regional stem growth on aspen forests across the west-central Canadian boreal forest, as a result of severe regional drought. Given the marked contrast in climatic conditions, the fact that the mean aspen height growth was similar between western and eastern portions of the study area is contrary to our research hypothesis. The latitude effect could explain a most productive aspen height growth observed with study stands located in the western boreal forest, despite a less abundant annual precipitation and an

important site water deficit in this portion. This effect is mainly reflected by lengthening the sunshine duration during the growing season in higher latitudes. Particularly in BC where study stands are located on the northeastern part of the province (Fig. 3.1), mean aspen height growth was closer to that of QC in the eastern Canada. These aspen stands in BC are in a forested biogeoclimatic zone in which Chen *et al.* (1998a) have reported that the frost-free period and precipitation during the growing season increase with latitude and decrease with elevation from Dawson Creek to Fort St. John to Fort Nelson. Consequently, lengthening the sunshine duration as well as longer and wetter growing season might have contributed to a higher aspen productivity in higher latitudes of western Canada.

The best predictive model (Mod1, Table 3.3) explained 40 % (R^2 adjusted: 0.4) of the observed variability in aspen height growth across the study area. This relatively moderate proportion suggests that the factors limiting aspen height growth vary from one location to another along the study area. Directly (by the precipitation regime) or indirectly (by the latitude effect), climate was the major factor controlling the variability in aspen height growth, comparatively to local soil conditions through the soil P availability (Table 3.4). However, some studies (e.g. Ens *et al.* 2013) have demonstrated that for tree species very productive and demanding in nutrients, soil effect can mask the effect of climate even at the landscape scale. Indeed, aspen growth can be reduced when the soil water availability (e.g. Hogg *et al.* 2013) or soil nutrient availability (e.g. Paré *et al.* 2001) becomes critical.

This study showed a significant negative effect of water deficit on aspen height growth, corroborating the results of other studies in the North American boreal forest (Hogg *et al.* 2005; Hanna and Kulakowski 2012; Hogg *et al.* 2013; Anyomi *et al.* 2015). Many other studies reported drought-related impacts on forests, as resulting in decreases in forest growth (Beck *et al.* 2011), net primary production (Bunn et al. 2007) and net biomass increment (Ma *et al.* 2012; Chen and Luo 2015). The

precipitation-related factors are most important drivers of aspen height growth along the east-west transect of boreal Canada. Site water deficit was the first significant variable to be included in the predictive model; however, its variability was completely explained by annual precipitation when the latter variable was subsequently added in the model, and the former removed due to statistical collinearity between these two variables. Forests respond indirectly to precipitation through the effect of soil moisture (Gauthier *et al.* 2014). The study result suggests that in a climate where the contrast between drier and wetter regions is expected to be more pronounced (IPCC 2013) in the future, ongoing global warming could exacerbate the negative impacts of climate on aspen productivity in most of interior and western Canada especially in the boreal transition area already drought-proned.

Latitude is a climatic surrogate variable likely to affect aspen height growth in different ways from a boreal region to another. The inclusion of site information such as spatial coordinates (longitude, latitude, and elevation) which are generally related to microclimatic effects, has the benefit of enhancing the prediction of growth across the study area. In current study, aspen height growth increased positively with latitude. The positive effect of latitude on aspen height growth may be attributable primarily to the study stands located in western boreal forest, as already explained above. Chen *et al.* (1998a) have also found an increase of aspen SI with latitude in the moist and warm Boreal White and Black Spruce subzone; and conversely, aspen SI decreased with increasing latitude in the Interior Douglas-Fir subzone (Chen *et al.* 2002), among the forested biogeoclimatic zones in British Columbia.

In terms of soil fertility, soil phosphorus availability was also found to be an important factor regulating aspen height growth. The positive effect of phosphorus shows that low aspen height growth in some study stands may be also attributed to P deficiency (Liang and Chang 2004; Pinno and Bélanger 2009; Pinno *et al.* 2010). Phosphorus can interact with other elements such as nitrogen (N) to affect positively

the nutrition and growth of hardwood species (Liang and Chang 2004). However, unlike us, Chen *et al.* (1998a) found that available P in mineral soil was negatively correlated with forest productivity in the northeastern BC. We believe this negative relationship resulted from techniques used to determine the true amount of plant-available P in the mineral soil; or else could be due to P locked into biomass in most productive sites where standing biomass would be the highest –drawing most available soil P. Kayahara *et al.* (1995) suggested that such a pattern may be the result of luxury consumption of P on N-poor, low-productivity sites.

The lack of a significant correlation of aspen height growth with other soil factors could be explained by (i) the special attention given to selection of mesic sites, which would have more or less comparable growing conditions in terms of soil C:N ratio, pH, exchangeable cations and texture. The range of variation in these environmental measurements among the study stands does not seem large enough to have a significant correlation with aspen SI; and (ii) the ability of aspen to improve site productivity with its high nutrient cycling rate (Legaré *et al.* 2005a); in contrast to black spruce that regardless of the situation contributes to deteriorating the site quality through paludification processes (Fenton *et al.* 2005).

3.6 Conclusion

At the study gradient scale, aspen height growth varied as a function of site conditions including climate interacting with local soil properties. Climate played a major role in determining aspen height growth. Precipitation has been identified as the most significant climate factor driving this growth, with low aspen productivity in central region of Canada due to high water deficit. Since the boreal ecosystems are particularly sensitive to climatic variations, the increase in the drought severity expected in boreal regions due to global warming could accentuate the decline in aspen productivity in affected areas, especially in central Canada. The climate pre-

eminence in the aspen growth is because of the very wide study scale; however, within a given region with minimal differences in climate, aspen productivity would be likely controlled locally by soil and site variables.

3.7 Acknowledgements

We thank Dave Gervais (NRC, Laurentian Forestry Centre) and the whole team of "Aspen project" of UQAT-UQAM Industrial Chair in Sustainable Forest Management for the fieldwork; CIPHA project managers (NRC, Northern Forestry Centre) for providing information and access to the CIPHA network in Western Canada, David Paré's team (NRC, Laurentian Forestry Centre) for assistance in sampled soils analysis in the laboratory; Rémi St-Amant (NRC, Laurentian Forestry Centre) for assistance with the climatic data; Annie-Claude Bélisle (PhD student-UQAT) and trainees student for assistance in stem analysis; and Mélanie Desrochers (Research professional - CEF) for map of study area.

Figure 3.1 Map of the study area with aspen stand locations shown. Each small black square represents a sampled aspen stand.

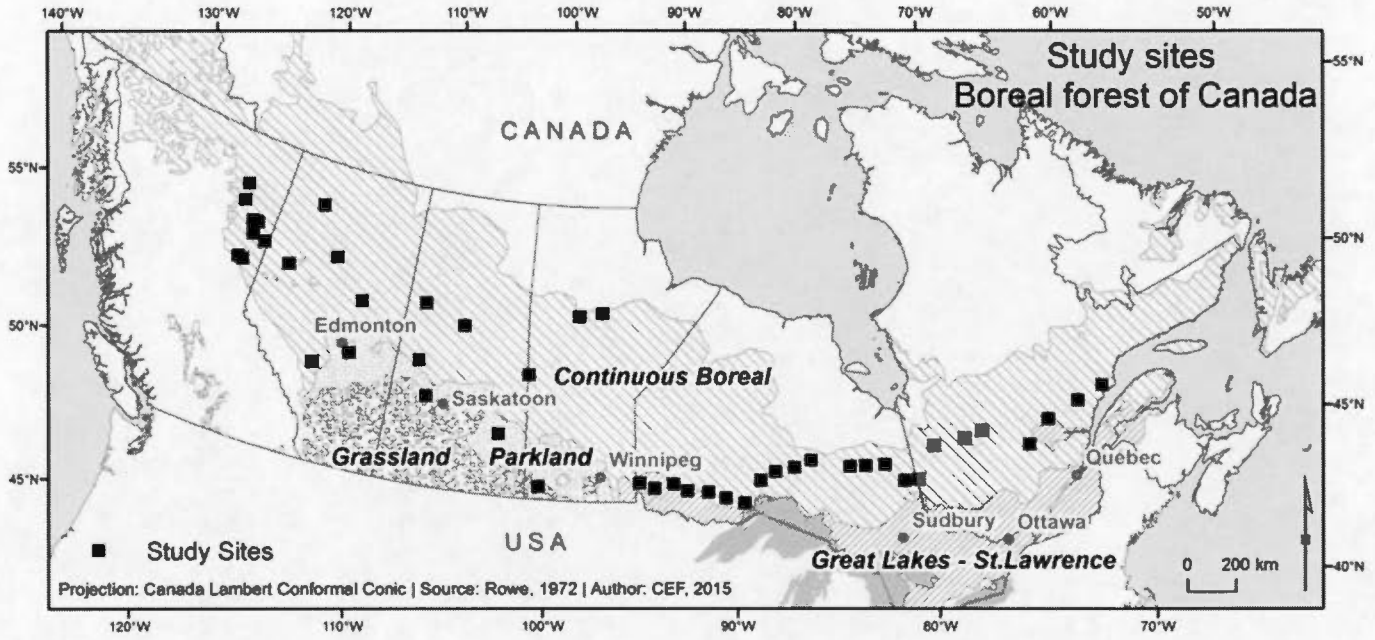

Table 3.1 Description of climate conditions, tree and stand characteristics, and mineral soil properties. To illustrate the longitudinal gradient, stands were grouped by provinces. Each mean (± standard deviation) has been calculated from number of stands.

	Provinces [a]					
	BC	AB	SK	MB	ON	QC
Number of stands [b]	11	6	5	4	15	8
Spatial gradient						
Longitude (W)	120°16'-122°45'	112°56'-118°16'	103°10'-108°47'	97°10'-101°41'	80°10'-94°56'	67°59'-79°25'
Latitude (N)	55°25'-58°07'	52°36'-58°20'	51°19'-55°45'	49°29'-56°02'	48°34'-49°58'	48°29'-49°34'
Elevation (m)	564-750	343-1028	444-710	233-436	195-503	286-526
Tree and stand characteristics						
Aspen Site Index at 50 yrs (m)	19.1 ± 2.2	18.4 ± 2.3	14.9 ± 3.5	14.6 ± 2.4	18.9 ± 3.7	20.4 ± 3.8
Stand age (yrs.)	60.1 ± 7.8	65 ± 5.7	73.6 ± 8.3	80.2 ± 7.0	80.2 ± 11.6	76.7 ± 15.5
Aspen basal area ($m^2 \cdot ha^{-1}$)	16.2 ± 14.3	25.9 ± 12.5	23.0 ± 8.5	27.4 ± 8.0	38.8 ± 7.4	39.1 ± 8.6
Total basal area ($m^2 \cdot ha^{-1}$)	16.3 ± 14.3	27.7 ± 11.2	24.1 ± 9.8	28.7 ± 8.1	43.6 ± 9.6	45.1 ± 8.8
Stand density (stems.ha^{-1})	704.5 ± 286.3	1158.3 ± 554.0	710.0 ± 312.5	1037.5 ± 463.0	940.0 ± 250.9	1170.3 ± 306.2
Climatic characteristics						
MAT (°C)	1.5 ± 1.0	1.8 ± 1.2	1.3 ± 0.8	-0.1 ± 2.8	1.8 ± 0.8	0.9 ± 0.4
MAP (mm)	519.2 ± 42.0	459.3 ± 61.7	456.5 ± 32.0	467.0 ± 20.2	758.0 ± 63.8	934.5 ± 48.6
H° (%)	68.1 ± 0.8	69.8 ± 1.0	71.9 ± 1.2	71.6 ± 1.6	73.2 ± 1.2	74.1 ± 0.8
GDD (°C.d)	2130.9±112.5	2276.6±88.4	2317.1±120.6	2288.2±412.6	2424.4±180.5	2191.1±101.4
WD (mm)	99.1 ± 27.8	116.4 ± 29.1	117.1 ± 12.0	110.5 ± 31.8	53.8 ± 9.8	27.4 ± 5.6
Mineral soil properties						
C:N ratio	13.4 ± 1.7	12.9 ± 1.2	20.1 ± 13.5	17.6 ± 8.8	37.1 ± 36.4	19.4 ± 3.4
pH (water)	4.9 ± 0.8	5.6 ± 0.4	5.9 ± 0.7	7.1 ± 0.9	5.8 ± 0.7	5.2 ± 0.2
Phosphorus (Bray II, mg/kg)	2.7 ± 2.7	9.3 ± 9.3	2.0 ± 2.1	3.7 ± 2.1	4.1 ± 4.0	4.3 ± 4.9
CEC (cmol(+)/kg)	5.9 ± 3.3	14.0 ± 9.0	5.8 ± 5.1	30.2 ± 9.7	7.4 ± 13.1	3.0 ± 3.2
tSand (%)	53.1 ± 41.5	38.5 ± 15.7	65.2 ± 11.5	34.4 ± 26.4	60.5 ± 21.7	41.9 ± 27.0
tSilt (%)	33.8 ± 31.8	37.7 ± 8.9	21.9 ± 6.7	20.0 ± 3.7	26.7 ± 14.4	29.8 ± 18.5
tClay (%)	13.1 ± 9.7	23.8 ± 13.7	12.9 ± 7.5	45.6 ± 28.8	12.8 ± 15.1	27.5 ± 30.2

[a] BC (British Columbia), AB (Alberta), SK (Saskatchewan), MB (Manitoba), ON (Ontario) and QC (Quebec). [b] The number of aspen-dominated stands sampled by province in Canada. The abbreviations of variables are described in the text (in Material and methods section).

Table 3.2 Pearson's correlation coefficient (r) between aspen site index (SI) and all environmental factors used as predictors, and among the environmental factors.

	Spatial			*Climate*					*Soil physical and chemical properties*						
	Long	Lat	Elev	T°mean	P°	H°	DD	AI	C:N	pH	P	CEC	tSand	tSilt	tClay
aspen SI	-0.17	-0.04	-0.16	-0.08	**0.38**	0.05	-0.19	**-0.38**	0.10	-0.24	**0.37**	-0.16	0.07	0.09	-0.15
Long		**0.89**	**0.76**	0.13	**-0.89**	**-0.89**	-0.19	**0.77**	-0.28	-0.20	0.03	0.08	-0.05	-0.01	0.07
Lat			**0.54**	**-0.28**	**-0.79**	**-0.88**	**-0.52**	**0.65**	**-0.29**	-0.22	0.11	0.13	-0.24	0.01	0.28
Elev				**0.38**	**-0.57**	**-0.64**	-0.18	**0.49**	**-0.32**	**-0.40**	-0.25	-0.23	0.06	0.19	-0.22
T°mean					-0.02	0.00	**0.73**	0.21	-0.04	-0.01	-0.06	-0.15	**0.32**	0.08	**-0.44**
P°						**0.73**	0.04	**-0.91**	0.24	-0.11	-0.06	-0.28	0.05	0.15	-0.17
H°							**0.30**	**-0.63**	0.24	**0.30**	-0.10	-0.03	0.12	0.08	-0.21
DD								0.13	0.13	**0.35**	0.13	0.05	**0.43**	-0.26	**-0.33**
AI									-0.24	0.24	0.10	**0.34**	-0.07	-0.05	0.12
C:N										0.20	0.09	0.03	**0.35**	**-0.40**	-0.13
pH											0.08	**0.75**	-0.26	-0.11	**0.39**
P												0.14	0.05	-0.09	0.01
CEC													**-0.52**	0.00	**0.62**
tSand														**-0.56**	**-0.79**
tSilt															-0.06

Boldface indicates a significant correlation (n = 49, P < 0.05).

Table 3.3 Selection of multiple regression models based on AICc for aspen height growth along the pan-Canadian gradient.

Candidate models	Model ID	K	LL	AICc	ΔAICc	W_i	R^2 adjusted	*P* -value
MAP+Lat+P	**Mod1**	**5**	**-111.44**	**234.28**	**0.00**	**0.54**	**0.40**	**< 0.001**
WD+Lat+P+MAP+MAT	Mod2	7	-109.79	236.32	2.03	0.20	0.42	< 0.001
WD+Lat+P+MAP	Mod3	6	-111.42	236.84	2.56	0.15	0.39	< 0.001
WD+Lat+P+MAT	Mod4	6	-112.69	239.38	5.09	0.04	0.36	< 0.001
WD+Lat+P	Mod5	5	-114.5	240.4	6.11	0.03	0.32	< 0.001
WD+P+H°	Mod6	5	-114.83	241.05	6.77	0.02	0.32	< 0.001
MAP+Lat	Mod7	4	-116.19	241.29	7.00	0.02	0.29	< 0.001
WD+P	Mod8	4	-116.74	242.39	8.10	0.01	0.28	< 0.001
WD	Mod9	3	-121.93	250.39	16.1	0.00	0.12	0.008
MAP	Mod10	3	-121.94	250.41	16.13	0.00	0.12	0.008

K: the parameter count includes intercept and variance; LL: the log-likelihood value of the model; AICc: the second-order Akaike Information Criterion value, for small sample sizes; ΔAICc: the delta AICc, a measure of each model relative to the most parsimonious model; and W_i: the Akaike weights, representing the ratio of the ΔAIC of a given model relative to the whole set of R candidate models; models are ranked based on their AIC scores, where the smallest AIC represents the best model (in bold).

Table 3.4 Model-averaged estimates of the explanatory variables of the parsimonious model and their 95% confidence intervals (CI), as well as their variance partitioning.

Parameters	Estimate	Lower CI	Upper CI	SE	Pr (>|t|)	Variance (%)
MAP	0.015	0.009	0.021	0.003	< 0.001	74.1
Lat	0.59	0.255	0.924	0.171	0.001	40.5
P	0.227	0.084	0.371	0.073	0.003	33.3

SE, standard error. Variance (%) includes the proportion of explained variance which is intrinsic to the variable and that of his interaction effect with the other variables in the model.

CONCLUSION GÉNÉRALE

Cette recherche doctorale constitue une contribution significative à notre compréhension et à la connaissance de la forêt boréale canadienne dominée par le tremble. Bien qu'en grande partie descriptive, cette recherche apporte des éléments nouveaux et est particulièrement originale à l'effet qu'il s'agit d'une des premières études synthétisant l'information sur la régénération coniferienne, la structure et la composition, et la croissance en hauteur des peuplements dominés par le tremble sur un énorme transect au Canada. Elle visait à mieux comprendre les relations entre le climat, les régimes de perturbations, la croissance et la dynamique du tremble dans la forêt boréale du Canada, dans un environnement climatique en constante évolution. L'incidence directe (climat) ou indirecte (régimes de perturbation) du réchauffement climatique pose des préoccupations pour les utilisateurs du tremble, et comment la productivité et la dynamique naturelle des peuplements de cette espèce pourraient être affectées dans le futur sous le changement climatique. En effet, il existe des études régionales qui mettent en évidence une expansion des tremblaies pures en forêt boréale du Canada, qui serait associée aux impacts dus à la récolte (par ex. Laquerre *et al.* 2009) ou encore qui traduirait davantage des impacts de feux d'origine humaine (par ex. Grondin *et al.* 2014). Des études rapportent également une augmentation à grande échelle de la mortalité des tiges de tremble, du déperissement et de la diminution de la croissance des tremblaies en Amérique du nord, attribuables aux impacts liés notamment au stress hydrique (ex. Hogg *et al.* 2008, Worrall *et al.* 2010). Les écosystèmes boréaux étant particulièrement sensibles aux variations du climat.

Spécifiquement, cette recherche avait pour objectif d'évaluer les effets de la variabilité climatique et de régimes de perturbations sur la croissance et la dynamique du peuplier faux-tremble, en échantillonnant le long d'un gradient longitudinal d'un

bout à l'autre de la forêt boréale mixte du Canada. Dans ce territoire d'étude, les variations de précipitations et de régime de feux subséquent en constituent les principaux gradients environnementaux. Même si les prédictions climatiques prévoient une augmentation de la température et des précipitations dans certaines régions boréales du Canada, les augmentations prévues des précipitations dans les plaines boréales (zone intérieure de l'ouest canadien) seraient insuffisantes et ne pourraient totalement compenser pour l'augmentation de l'évapotranspiration induite par l'augmentation des températures. Ce stress hydrique est prévu pour être plus important dans la partie Ouest de la forêt boréale (Price *et al.*, 2013). Il était donc attendu que les résultats de ce doctorat donneraient un aperçu sur la façon dont les changements climatiques pourraient affecter les forêts de tremble ou des espèces équivalentes à un endroit donné, si l'enveloppe climatique de ce dernier endroit venait à changer dans des dimensions comparables à celles observées à un autre endroit de la région d'étude. Pour ce faire, les principaux résultats de cette recherche montrent que :

(1) *De la Régénération coniferienne dans les tremblaies :*

La distribution spatiale de la régénération résineuse dans les tremblaies, le long du gradient longitudinal dans la forêt boréale mixte du Canada, suit un patron en forme de U.

Dans la portion ouest du gradient de l'étude (correspondant aux provinces de l'Alberta et de la Colombie-Britannique), la proportion de tremblaies ayant de la régénération résineuse en sous-couvert (essentiellement de l'épinette blanche) était plus élevée contrairement à notre hypothèse de recherche. Ce qui est tout de même surprenant au regard des conditions climatiques plus sèches et de la dominance de grands feux plus fréquents qui caractérisent cette partie de la forêt boréale. Le climat et le régime de feu associé ne semblent donc pas être les facteurs qui gouvernent la

distribution actuelle de la régénération résineuse dans les peuplements de l'ouest du Canada.

Tant par son abondance que par sa fréquence d'occurrence, l'épinette blanche dans les tremblaies de l'ouest canadien apparaît omniprésente (Cumming *et al.*, 2009). Cette dominance de la régénération de l'épinette blanche dans les tremblaies de l'ouest du Canada semble contraire à l'autécologie de cette espèce conifèrienne, en demontrant une certaine adaptation aux cycles de feu courts et aux conditions climatiques plus sèches dans cette partie du gradient. L'une des hypothèses les plus plausibles qui expliqueraient cette distribution de l'épinette blanche dans l'ouest semblent être celle du "leg biologique": l'abondance actuelle de l'épinette blanche dans le sous-couvert des tremblaies de l'ouest canadien serait le reflet de son abondance passée suite à la déglaciation au cours de l'holocène et des patrons subséquents d'intrusion des essences forestières (Williams *et al.*, 2004). D'autre part, la genèse des sols est extrêmement variée d'Est en Ouest du Canada; passant de podzols et brunisols éluviés acides à l'Est, à des chernozems et luvisols au centre, et des brunisols et des podzols humiques à l'Ouest. L'incohérence apparente entre un climat sec dans l'ouest canadien et la présence abondante de l'épinette blanche pourrait être en partie attribuable au fait que cette espèce occupe la fraction la plus humide des sols dans cette portion du transect. L'épinette blanche serait présente sur des dépôts à texture plus fine (argile, loam argileux) ou sur des dépôts sableux ou limoneux recoupés par des couches d'argile. Le sol argileux (rétention de l'eau plus forte) étant prédominant dans les paysages de l'Ouest canadien où peu d'eau est disponible, des pédologues ont observé de très fortes relations entre l'argile et l'occurrence de l'épinette blanche dans l'ouest Canadien [*Communication personnelle*, Nicolas Bélanger, 2016]. Les conditions des sols favorables semblent expliquer en partie la dynamique de cette espèce résineuse dans l'ouest du Canada, en dépit de feux et de des conditions climatiques peu favorables (climat séc). L'épinette noire est une espèce conservatrice et peut croitre sur divers types de sols, alors que le

sapin baumier a des exigences nutritionnelles relativement élevées pour une essence résineuse.

Dans la portion centrale du gradient (correspondant aux provinces du Manitoba et du Saskatchewan), la régénération des conifères était particulièrement faible dans le sous-couvert des tremblaies. Autrement dit, la proportion de tremblaies sans régénération résineuse était plus élevée dans le centre du gradient. Cette faible régénération résineuse observée peut être attribuable à une combinaison de facteurs potentiels. Il y a notamment :

(i) la récurrence des grands feux sévères qui limiterait la régénération résineuse (McIntire *et al.*, 2005; DeMoor *et al.*, 2010) pour les tremblaies situées dans la partie nord; et l'empiètement de la prairie sur le sous-bois des tremblaies situées dans la partie sud, avec l'envahissement du sous-bois par des graminées (*calamagrostis canadensis* (*Michx.*)) qui créent une compétition sur la croissance et la survie de semis de conifères (Landhäusser and Lieffers, 1998);

(ii) l'indice d'aridité (c.à.d. le déficit en eau mensuellement accumulé) très élevé dans cette région, qui pourrait faire en sorte que des fréquents stress hydriques au moment de la germination ou au cours du développement des semis peuvent nuire à leur survie et entrainer une mortalité importante susceptible de limiter ou d'inhiber la régénération résineuse; et

(iii) la pression due au broutage des semis par les herbivores (Martin and Baltzinger, 2002; Potvin et al., 2003; Tremblay et al., 2007). Cette dernière hypothèse est plausible compte tenu des fortes populations de Cerf de virginie dans ces provinces, mais difficile à démontrer avec les données de l'étude.

Dans la portion Est du gradient (correspondant aux provinces du Québec et de l'Ontario), cette étude a montré que même s'il y avait dominance de régénération

résineuse (constituée de sapin et d'épinette noire) dans les tremblaies, bon nombre de ces dernières (32 %) apparaissaient dépourvues de régénération des conifères tolérants, contrairement à ce qui était attendu. L'allongement du cycle de feu dans cette partie Est du gradient devrait, en principe, favoriser le vieillissement des forêts et une augmentation des conifères tolérants à l'ombre à l'échelle du paysage (Lesieur *et al.*, 2002). Cette situation de tremblaies dépourvues de régénération des conifères tolérants apparaît généralement associée aux milieux ruraux et aux zones agricoles. Cela se traduit par une augmentation de la densité de routes autour des sites de l'étude et un faible éloignement de ces derniers aux zones agricoles avoisinantes, suggérant donc une augmentation des activités anthropiques dans cette région et leur impact potentiel sur l'écosystème forestier. En effet, l'intensification de la récolte du bois et des activités d'aménagements de forêts entreprises au cours des dernières décennies serait à la base de cette diminution de la régénération résineuse dans la partie Est du gradient. La pression anthropique a affecté sensiblement la distribution de la régénération résineuse dans les tremblaies de la partie Est du gradient, au point d'en affecter leur dynamique naturelle.

(2) *Variabilité de la structure et de la composition de tremblaies à travers le Canada :*

La description du portrait des régions de la forêt boréale mixte a montré que nos hypothèses de départ n'ont pas été complètement rencontrées, par rapport aux deux caractéristiques forestières analysées (structure et composition des peuplements).

Dans la partie Est du gradient (les provinces du Québec et de l'Ontario), les résultats de cette étude ont montré que la structure de tremblaies n'était plus en équilibre avec le régime de perturbations naturelles qui dominent dans cette région de forêt boréale. En effet, l'analyse de données d'inventaires forestiers indiquent que les tremblaies à structure juvénile sont plus abondantes comparativement aux tremblaies à structure mature dans la partie Est du Canada, malgré les conditions climatiques et le régime

naturel de feux (cycle de feu long) susceptibles de favoriser le vieillissement des forêts dans cette région. Cette faible proportion de tremblaies à structure mature et en corollaire la dominance de tremblaies à structure juvénile dans l'Est du Canada, serait davantage le reflet d'un historique plus ancien d'aménagement et d'utilisation de la ressource ligneuse que dans les autres provinces canadiennes. Ce résultat vient appuyer l'hypothèse de l'impact de l'homme sur le développement de l'écosystème qui avait été observée dans le chapitre 1. L'action de l'homme serait la principale raison de la simplification de la structure de tremblaies dans cette partie Est de la forêt boréale du Canada. Même si plusieurs tremblaies apparaissent avoir été altérées par les activités humaines, nos résultats indiquent que nombre d'entre-elles y ont toutefois conservées leur mixité.

Dans le centre et l'ouest du gradient de l'étude, la structure et la composition des tremblaies reflètent un certain équilibre avec les régimes de perturbation naturelle. Il y a plus de tremblaies de composition pure au centre (Manitoba et Saskatchewan) où l'activité du feu était globalement plus élevée, en comparaison avec la partie ouest du gradient (Alberta et Colombie-Britannique). En termes de structure de forêts, la proportion des tremblaies à structure mature semble être relativement plus élevée au centre qu'à l'ouest du gradient de l'étude, en raison vraisemblablement des forêts de tremble situées dans l'écorégion de la transition boréale, un écotone situé entre la forêt boréale au nord et les prairies au sud et où les événements de grands feux sévères sont moins fréquents. En effet, bien que le cycle de feu moyen soit globalement plus court au centre du canada, il apparait un certain contraste dans le régime de feu au sein de cette portion du gradient. Sa partie nord est dominée par des larges feux récurrents, alors que la limite sud de cette forêt brûle à peine (soit une plage maximale de cycle de feu > à 1000 ans). Il ressort donc de ces résultats que le bout du gradient entre le centre et l'ouest du Canada corrobore en partie notre hypothèse de recherche qui suggère une dominance de tremblaies matures dans les

régions à cycle de feux long, et inversement une dominance de tremblaies juvéniles dans les régions à cycle de feux court.

En outre, les résultats ont montré que le développement structural des tremblaies n'est pas uniquement fonction de l'âge du peuplement. Autrement dit, le régime de feu seul n'est pas suffisant pour prévoir la distribution de types structuraux attendus dans une région donnée. Il y a également la richesse du sol qui est capable de masquer la relation entre la structure et le régime de feu. En effet, la richesse du sol affecte directement le taux de croissance des arbres; et par conséquent, elle a une incidence directe sur la rapidité avec laquelle un peuplement change de structure au cours du temps. Les arbres vont croître plus rapidement sur des sites riches (recrutement plus rapide des grosses tiges) que sur des sites pauvres; ce qui implique que le changement de structure va s'opérer plus vite sur des sites riches par rapport aux sites pauvres. L'effet de la richesse du sol sur la structure de forêts apparaît évident lorsqu'on compare les tremblaies de l'Alberta à celles de la Colombie-Britannique. Les résultats de cette étude montrent que même si les tremblaies de la Colombie-Britannique sont âgées (moyenne d'âge = 69.2 ans), elles continuent de présenter une structure en majorité juvénile. Les tremblaies de l'Alberta même si elles sont plus jeunes (moyenne d'âge = 35.3 ans), affichent une structure à dominance mature. Ces deux provinces, quoique similaires en régime de feu, se comportent différemment pour la distribution des types structuraux, principalement en raison de leurs conditions de croissance.

Les résultats du chapitre 2 viennent en appui aux résultats du chapitre 1 quant à l'influence de l'homme sur la dynamique des tremblaies dans l'Est canadien. Ces résultats suggèrent que les activités humaines peuvent découpler le lien entre le régime de perturbations naturelles et l'écosystème, en superposant un nouveau régime de perturbations sur le régime naturel préexistant. Outre les effets de l'homme et du régime de feu, il y a également la richesse du site (conditions du sol) qui s'additionne

comme un facteur important affectant la vitesse de maturation structurale des forêts et dans une certaine mesure leur composition.

(3) *Variabilité dans la croissance en hauteur du tremble à travers le Canada :*

Dans l'ensemble, la productivité des tremblaies était meilleure dans les parties Est et Ouest du Canada, tandis qu'elle était moindre dans la partie centrale du gradient de l'étude. Le modèle prédictif indique que la croissance du tremble résulte de l'interaction entre le climat régional et les conditions du sol. Dans cette étude, la productivité des tremblaies est sous l'influence positive des précipitations, de micro-conditions environnementales liées au gradient latitudinal et de la disponibilité en phosphore dans le sol. En raison de sa forte corrélation avec le régime de précipitation, le déficit hydrique affecterait négativement la croissance du tremble. Le modèle explicatif de la distribution spatiale de la croissance révèle combien il est complexe de prévoir précisément la productivité des tremblaies à l'échelle du Canada. Bien que significatif, le meilleur modèle prédictif de l'étude n'a permis d'expliquer que 40 % (R^2 ajusté de 0.40) de la variabilité de la productivité que l'on observe le long du gradient pan-canadien. Cette proportion relativement modérée de la variabilité expliquée serait principalement due au fait que la productivité en forêt boréale peut être contrainte par un seul facteur. Le déficit de ce facteur peut entraîner une baisse dans la croissance de l'arbre. Ainsi, ce résultat de l'étude suggère que le facteur limitant la croissance du tremble n'est pas le même d'une province à l'autre du Canada. Il varie d'un endroit à un autre le long du gradient longitudinal à travers la forêt boréale. Par exemple, si la baisse de la productivité moyenne du tremble dans la partie centrale du gradient de l'étude pourrait être attribuable au déficit en eau, le facteur contraignant la croissance de cette espèce pourrait être la disponibilité en phosphore ou en azote dans une autre partie de la zone d'étude.

Il se dégage des connaissances acquises que la prévision de la réponse de tremblaies aux changements climatiques doit prendre en compte plusieurs éléments qui revêtent

une spécificité locale. Ces spécificités locales viennent brouiller l'interprétation que l'on peut faire de la réponse de cet écosystème face aux changements climatiques. Ces spécificités se traduisent notamment par (*i*) la distribution de la régénération résineuse qui serait contrôlée par le climat et les régimes de perturbations dans le centre du Canada, alors qu'elle serait plutôt une conséquence du leg biologique dans la partie Ouest du gradient. Tandis que dans la partie Est du gradient, cette distribution était fortement modelée par l'effet de l'homme; (*ii*) l'historique d'aménagement forestier et de la récolte du bois, qui a conduit à une simplification de la structure et de la composition dans les tremblaies de l'Est du Canada; (*iii*) la richesse du sol qui affecte le taux de croissance des arbres, et par conséquent, la vitesse de changement de la structure de forêts; et (*iv*) le facteur limitant la productivité du tremble, lequel varie d'une région à l'autre dans la forêt boréale, bien que le déficit en eau s'est révelé comme un facteur majeur de réduction de croissance.

(4) *Retombées scientifiques et les recherches futures :*

De tout ce qui précède, il apparait désormais difficile d'interpréter les effets de changements climatiques sur le recrutement des conifères, la structure et la composition des tremblaies, sans tenir compte des effets superposés des activités anthropiques. Cette dimension de l'homme est devenue essentielle, si l'on veut prévoir adéquatement la réponse de la végétation aux changements climatiques. Outre cette dimension humaine, il apparait aussi indispensable d'intégrer les autres spécificités évoquées ci-haut dans les paramètres d'analyse pour mieux prédire les effets de changements climatiques sur les caractéristiques des écosystèmes boréaux en général, et sur celles des peuplements dominés par le tremble en particulier.

Les analyses et interprétations écologiques de cette recherche étaient essentiellement basées sur des hypothèses du climat et des régimes de perturbations, en raison de l'échelle spatiale de l'étude. Cependant, une partie de la variation observée dans la distribution de la régénération résineuse et celle de types structuraux des tremblaies

de l'étude, le long du transect pan-canadien, serait expliquée par des facteurs environnementaux non inclus dans cette étude et ayant un effet à l'échelle locale. Il s'agirait notamment des variables du sol, la composition initiale du peuplement, la composition des peuplements du voisinage pour la disponibilité de semenciers, l'heritage structural des perturbations passées, ainsi que les données de perturbations secondaires tel que le régime d'épidémies d'insectes. En effet, la régénération d'espèces coniferiennes dans un site sérait influencée par la sévérité locale de la dernière perturbation (Frelich, 2002) ou encore par les effets de voisinage (Taylor et Chen, 2011). De plus, Anyomi *et al.* (2015) ont montré que la texture du sol et le type d'humus sont deux variables du site importantes et qui expliquent le mieux la productivité des tremblaies au Canada. L'importance de ces facteurs environnementaux locaux (par exemple : données de sol, composition du voisinage, historique d'épidémies de livrée de forêt sur le site) pour la dynamique de la régénération coniferienne (dans le chapitre 1) et/ou la structure forestière (dans le chapitre 2) des tremblaies de l'étude devrait être investiguée de manière approfondie avec des nouvelles recherches à entreprendre. Ces nouvelles approches analytiques seraient intéressantes, étant donné que les aménagistes forestiers prennent leurs décisions à l'échelle locale. Dans le cadre du chapitre 3 sur la croissance en hauteur du tremble, il serait aussi intéressant de tester la robustesse de notre modèle explicatif final (combinant précipitation, latitude, et disponibilité en phosphore) : (a) en augmentant le nombre d'observations (replicats de sites) le long du gradient de l'étude; (b) en développant des modèles régionaux (portions est, centre et ouest du transect longitudinal du canada); et (c) en excluant de l'analyse, les sites localisés dans le parc à peuplier.

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